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BEHAVIORAL RESPONSE TO MULTI-CHANNEL ENVIRONMENTAL NOISE:
TRACKING NOISE-INDUCED CHANGES IN DAILY LOCOMOTOR PATTERNS AND
MATE ATTRACTION STRATEGIES IN *ACHETA DOMESTICUS*

BY

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THESIS

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This thesis/dissertation was examined and approved in partial fulfillment of the requirements for the degree of Master of Science in Integrative and Organismal Biology by:

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On January 31st, 2020

Approval signatures are on file with the University of New Hampshire Graduate School

Dedication

I would like to dedicate this work to Steve Irwin, better known as “The Crocodile Hunter.” His passion for all animals, especially the unlovable ones, has been a constant source of inspiration for me since childhood. It is because of him that I chose my path in life.

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ABSTRACT

BEHAVIORAL RESPONSE TO MULTI-CHANNEL ENVIRONMENTAL NOISE: TRACKING NOISE-INDUCED CHANGES IN DAILY LOCOMOTOR PATTERNS AND MATE ATTRACTION STRATEGIES IN *ACHETA DOMESTICUS*

By

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Communication is essential in biotic systems, and signals represent information exchanged between a sender and receiver. Noise can interfere with the transmission, detection, and processing of signals, and can occur in any sensory channel. Noise can also disrupt behaviors related to foraging, predator detection and avoidance, and social interactions. Most research on the effects of noise on animal behavior has been focused on its effects on terrestrial avian species and marine mammals in an isomodal context, with data on invertebrates generally sparse. Many insects have highly adapted structures for sound and vibration detection, and thus make ideal models for studying noise effects on behavior. In the following experiments, I used house crickets, *Acheta domesticus*, to answer the following questions: 1) Do different types and durations of noise influence the daily locomotor patterns in animals? 2) Do different types and durations of noise influence decisions related to male signaling?

To assess the effects of noise in three forms (isomodal, crossmodal, and multimodal) on locomotor patterns, I first recorded cricket locomotion in an activity monitor to establish a daily pattern, with a focus on identifying peak periods of activity. Crickets were then exposed to either noise only during this peak period (intermittent) or continuously across a 24-hour period. I found that all durations and forms of noise had an effect on *A. domesticus* locomotion, changing not only the daily pattern of locomotion, but the magnitude as well. All three forms of noise changed when crickets were

active, and just how active they were, highlighting the importance of noise conditions in the daily behavior of this species, and potentially other species of cricket, and other taxa. Crickets may endure fitness costs due to this change in activity.

To assess the effects of noise in three forms (isomodal, crossmodal, and multimodal) on male cricket signaling behavior, male calling was first recorded over the course of four days to identify peak periods calling times and the overall temporal pattern of male display. As in the first experiment, all noise treatments changed male calling behavior in both the time of day and magnitude of calling. In *Acheta domesticus*, accurate reception of the male's call by females is crucial, and mating opportunities could be missed when males change their calling behavior, as they have done here. Anthropogenic noise will only increase in the coming years, and further research is needed to understand the impact it may have on organism behavior and fitness.

INTRODUCTION

Animals must overcome many factors to survive and pass along their genes to the next generation. They must be able to find resources, and eventually a mate, while dealing with competition from conspecifics and heterospecifics, and avoiding predation. Prior to mating, animals must attract a mate, and can do so using visual, acoustic, tactile, and/or chemical signals alone or in combination. In species using acoustic communication, a sender must produce a signal that is propagated through the environment, and a receiver must be able to detect, identify and evaluate this signal to respond. Several factors can attenuate or otherwise alter the signal as it travels through the transmission medium, one of which is noise. Noise is broadly defined as energy or matter that occurs in the same sensory channel as a focal signal, can interfere with the transmission, detection, and processing of said signals (Zhao *et al.* 2017), and comes in many forms. Geophony (geophysical noise) is noise from non-living sources, such as wind, trees falling, or water rushing, and biophony is noise created by other animals (Pijanowski *et al.* 2011). Examples of biophony include the dusk chorus of insects and the dawn chorus of birds (Shannon *et al.* 2016, Francis *et al.* 2009, Schmidt and Balakrishnan 2014). Noise can also be anthropogenic (human-generated; technophony), can interact with multiple sensory modalities, and can influence animal behavior (Barber *et al.* 2010, Kight and Swaddle 2011, Luo *et al.* 2015). Isomodal noise interferes with communication in the same modality as the transmitted signal. For example, airborne traffic noise is known to mask parent-offspring acoustic communication in the blue tit, *Cyanistes caeruleus* (Lucass *et al.* 2016). Noise can also be found in the context of and interacting with other sensory channels. For example, acoustic noise can interfere with visual, chemical, and vibrational signals. This is known as crossmodal noise

(Vandersal and Hebets 2007, Halfwerk and Slabbekoorn 2015). Crossmodal noise is generally considered any disturbance that propagates via a different medium than that carrying a focal signal. For example, noisy surface ripples in water produced by wind and rain are detected by and influence male Tungara frogs, *Physalaemus pustulosus*, producing airborne sexual advertisement signals (Halfwerk *et al.* 2016). Noise can also be multimodal, interacting with multiple sensory channels at once (sound, visual, chemical, vibration). Anthropogenic noise often exhibits this multimodal complexity, and thus holds potential to influence animal behavior as a sensory pollutant (Halfwerk and Slabbekoorn 2015). Noise is considered an environmental stressor and can be equally as detrimental as other forms of pollution (Francis and Barber 2009). Many studies on the effects of noise in animals have been conducted with vertebrate model species, particularly birds and marine mammals (Shannon *et al.* 2016, Francis and Barber 2013, Miksis-Olds 2016, 2012, Miksis-Olds *et al.* 2009, Tyack 1999). Less attention has been paid to invertebrates, which account for 80% of the biomass on the planet (Mora *et al.* 2011). More information is needed on how invertebrates are influenced by noise, particularly insects, which often used airborne and substrate-borne sound to communicate; see Raboin and Elias (2019) and Morley *et al.* (2014) for recent reviews. Insects support the trophic structure of most ecosystems, and thus noise-induced perturbations to insect populations can upset and alter ecosystem function. While animal populations have the capacity to evolve solutions to fitness-related problems given sufficient time, the acoustic environment in many ecosystems has changed rapidly during the post-industrial revolution period. It is thus necessary to understand how human enterprises that produce noise affects animal populations, especially the oft-forgotten invertebrate. It is easy to observe and measure the direct impact humans have on ecosystems with respect to habitat destruction, hunting and poaching, and chemical pollution, but noise

pollution is one byproduct of human activity we often fail to consider when addressing the interactions within and across coupled human-natural systems.

Multimodal Communication and Noise

Many animals have been observed using multimodal communication, or communication across more than one sensory channel simultaneously (Partan 2017, Higham and Hebets 2013). This often occurs as a combination of airborne acoustic, visual, and vibrational signals, as is the case with jumping spiders (Girard *et al.* 2011, Elias *et al.* 2004, Elias *et al.* 2003), New Zealand weta (McVean and Field 1996, Howard *et al.* 2018), bush crickets (Rajaraman *et al.* 2015), red-winged blackbirds (Rios-Chelén *et al.* 2015, 2016), rock frogs (Grafe *et al.* 2012), cichlids (Maruska *et al.* 2012), and several other frog species (Wilson *et al.* 2013, Arch *et al.* 2011, Preininger *et al.* 2013). Multimodal communication has also been observed with a combination of visual and olfactory cues in webbing clothes moths, *Tineola bisselliella* (Takács *et al.* 2003). Predators may rely on elements of multimodal cues given off by prey animals to locate them (de Moraes *et al.* 2019, Rubi *et al.* 2019), and the ability to perceive these cues can be hindered by the presence of anthropogenic noise (Francis 2015). Fringe-lipped bats, *Trachops cirrhosis*, use sound and visual cues of male Tungara frogs', *Physalaemus pustulosus*, multimodal displays to locate them, relying more on visual cues (movements of the throat sac) when the environment is acoustically noisy (Rhebergen *et al.* 2015). The frogs themselves also use throat sac movement to find each other in noisy environments (Prininger *et al.* 2013). This “multimodal shift” can occur during production or reception of a signal (Partan 2016, Partan 2013). Sometimes, redundant information is sent across multiple modalities, and an animal can switch from a “noisy” channel to a “quiet” one. One species of wolf spider (*Schizocosa ocreata*) changes its courtship displays depending on ambient lighting conditions (Taylor *et al.* 2005), and three-

spined sticklebacks, *Gasterosteus aculeatus*, do the same depending on the clarity of the water (Heuschele *et al.* 2009). Grey squirrels respond to different cues depending on their habitat, with visual cues being more salient in a loud, urban environment (Partan *et al.* 2010). These sensory dependency shifts can be important when environmental conditions are variable. Anthropogenic sensory pollution, such as that produced by transportation and energy production, is often multimodal. For example, cars produce both airborne noise, substrate-borne vibration and chemical pollution, and the perception of these elements is also multimodal (Halfwerk and Slabbekoorn 2015). It is therefore informative and necessary to consider the multimodality of sensory pollution when assessing human impacts on animal behavior and populations.

Crossmodal Noise

When the processing of irrelevant environmental information in one sensory modality hinders processing of information in another modality, this is known as crossmodal noise (Halfwerk and Slabbekoorn 2015). In one study, light pollution decreased the response of moths to bat calls (Minnaar *et al.* 2015). When assessing the effects of crossmodal noise, it is important to understand how an animal perceives its environment. Crickets, for example, have auditory and substrate-borne vibration receptors in their legs, which lead to the prothoracic ganglion, and then to the brain (Counter 1976). One study on the field cricket, *Gryllus bimaculatus*, found that substrate-borne vibration inhibits the activity of the omega neuron in the leg, which affects the ability of the animal to perceive airborne sound (Wiese 1981). Similarly, anthropogenic noise has been shown to interfere with olfactory cues in mammals. When presented with road noise playbacks, mongoose, *Helogale parvula*, exhibited a lower response to the odor of predator feces than in the absence of noise. (Morris-Drake *et al.* 2016). Hermit crab shell selection relies on tactile, chemical, and visual perception. When crabs were exposed to noise, they spend less time

investigating and entering a new shell (Walsh *et al.* 2017). The cuttlefish, *Sepia officinalis*, uses complex visual signals for intraspecific communication. A study by Kunc *et al.* (2014) found that this species adjusted their visual displays in the presence of ship noise by changing color more frequently. There are also cases where crossmodal noise can be beneficial. A study on jumping spiders (Vandersal and Hebets 2007) found that crossmodal noise in the form of substrate borne vibration improved learning. Spiders were better able to avoid a heated square, indicated visually by color, than when vibration was present. This behavior continued even after the vibrational stimulus was removed. While additional work is required to understand sensory phenomenon like these, it is clear that crossmodal and multimodal noise can produce unexpected behavioral outcomes.

Physiological Effects of Airborne Noise

Chronic noise exposure has short and long-term effects on animal health. An extensive review of the effects of noise across taxa and physiological systems is presented by Kight and Swaddle (2011). One physiological system commonly affected is the neuroendocrine system. Stress response related to exposure to noise increases the production of particular hormones such as cortisol, epinephrine, and norepinephrine. Acute exposure to loud noises can cause the release of stress hormones (Francis and Barber 2013, Barber *et al.* 2010). This physiological response has been observed in seahorses (Anderson *et al.* 2011), chickens (Chloupek *et al.* 2009), and dogs (Gue *et al.* 1987). Reproduction and development can also be affected by exposure to noise. Male mice have shown lower testosterone levels with noise exposure, which adversely affects reproduction (Ruffoli *et al.* 2006). Developmental effects can be seen in the embryotic stage. Indian meal moth (*Plodia interpunctella*) larvae saw a 75% mortality rate of eggs exposed to noise (Kirkpatrick and Harein 1965), and Muscovy duck embryos (*Cairina moschata* f.

domestica) exhibited behavioral response to noise while still in the egg (Höchel *et al.* 2002). Rats have shown asymmetrical development when exposed to noise, which is an indicator of developmental instability (Møller and Swaddle 1997). Noise exposure also affects metabolism, as increased energy is needed for hormone production (Chloupek *et al.* 2009). The influence of environmental noise on the endocrine systems of insects has not been sufficiently studied, and thus we do not know if stress-related hormones are upregulated due to noise exposure. Additional research on this topic is warranted.

The heart contracts more rapidly and forcefully during stress responses (Herd 1991, Kight and Swaddle 2011), and this can lead to long-term cardiac problems. Heart damage has been seen in mitochondria of rat heart cells, changing their morphology and function, as a result of noise exposure (Gesi *et al.* 2002). The detrimental effects of noise on human cognition and sleep are well-studied and similar results can be seen in many non-human animals, with some effects becoming permanent. Song learning in birds is altered by noise due to hearing impairment (Marler *et al.* 1973). A study on zebra finches, *Taeniopygia guttate*, revealed that juvenile birds exposed to noise sang noisy and unstable songs that did not resemble their natural song (Funabiki and Konishi 2003). Because of noise's underlying effect as a stressor, cognition can also be affected by both acute and chronic exposure. A study involving rats exposed to noise found shifts in neuronal structure that likely explained poor performance in the Morris water maze test. (Cui *et al.* 2009). Auditory acuity and cochlear morphology may also be permanently altered by noise exposure. Hearing impairment and deafness can occur from a single event above the pain threshold (a single explosion for example), damaging the cochlea or related neural structures (Barber *et al.* 2010, Rabin *et al.* 2003) in vertebrates. One study in rats found temporary effects on the auditory processing of the brain (Sun *et al.* 2011), and another study

found that fish swim bladders may be torn or ruptured with noise exposure, which alters their perception of sounds and hinders buoyancy control (Popper and Hastings 2009). The short and long-term physiological effects of intense and/or prolonged exposure to noise in invertebrates is far less studied.

The stress of noise exposure can also affect the immune system, causing systemic response to noise. Lower thymus weights were observed in rat pups whose mother was exposed to noise while pregnant (Sobrian *et al.* 1997), while rats exposed to noise exhibited lower T cell counts (Dobbe 1996). Noise can also affect DNA integrity and genes in two ways: by setting off chemical cascades that lead to DNA damage, and by altering gene expression (Kight and Swaddle 2011). Rats that were exposed to noise performed poorly on spatial tasks and had decreased expression of NMDA receptors (Cui *et al.* 2009). GABA receptors in the central nervous system are also affected in noise-exposed rats (Lai and Carino 1990). While this review is extensive, the authors note underrepresented taxa, including reptiles, amphibians, and invertebrates. While mammals and birds often exhibit adverse effects due to noise exposure, additional research is required to understand how noise influences the physiology and behavior of insects and other invertebrates. Many insect species have co-evolved in noisy conditions, and thus selection has likely favored adaptive solutions to this ubiquitous problem.

Behavioral Effects of Airborne Noise

Animals alter their behavior in several ways in response to airborne noise. Noise can be a distraction, an irritant, or be perceived as a danger (Luo *et al.* 2015, Rabin *et al.* 2003, Francis and Barber 2013). Animals may avoid noise all together, and there are many examples of lower population levels near sources of anthropogenic noise (Barber *et al.* 2010, Proppe *et al.* 2013). A study on songbirds found reduced abundance near oil and gas extraction sites (Bayne *et al.*

2008), and there have been similar, though fewer findings in under-studied arthropods (Bunkley *et al.* 2017). Several other studies have found lower animal abundance near road traffic (with bird diversity in McClure *et al.* 2013; in the sage grouse, *Centrocercus urophasianus*, in a study by Blickley and Patricelli 2012). Foraging may also be affected by airborne noise, both due to reduced attention (noise as a distraction), and the inability to detect sounds made by prey, such as in echolocating bats. A study on Daubenton's bats, *Myotis daubentonii* (Luo *et al.* 2015) found that traffic noise reduced foraging efficiency in the bats, as they were unable to detect the sounds made by their rodent prey. This was also seen in the greater mouse-eared bat, *Myotis myotis* with insect prey (Siemers and Schaub 2010). In another study, fringe-lipped bats (*Trachops cirrhosus*) were observed to use more echolocation clicks while hunting in noise to compensate for this (Gomes *et al.* 2016). Common Chaffinches, *Fringilla coelebs*, spent more time exhibiting vigilance behavior (checking around them rather than pecking at food) in noise, resulting in a reduction in food intake (Quinn *et al.* 2006). Short-eared (*Asio flammeus*) and long-eared (*Asio otus*) owls have also shown a decrease in foraging efficiency with traffic noise, with the efficiency decreasing as the noise level increased (Senzaki *et al.* 2016). Hubert *et al.* (2018) found that fewer of the shore crab species *Carcinus maenas* were able to locate food items when presented with broadband artificial sound. Foraging effects can lead to physiological effects and cause further harm to animals in areas with high noise, both natural and anthropogenic. An animal's response to possible predation risk may also be affected in noise, as in the terrestrial hermit crab, *Coenobita clypeatus* (Aaden *et al.* 2010). Crabs took more time to respond to a visual cue (a predator) in the environment that included white noise.

Perhaps the behavior most influenced by airborne noise is acoustic communication. Many Animals rely on acoustic communication for mating and courtship, territorial displays and

defense, predator avoidance, and other social interactions (Rabin *et al.* 2003, Zhao *et al.* 2017, Partan 2017). Acoustic (airborne) signal propagation is affected by temperature, humidity, foliage, and topography (Rabin *et al.* 2003). These factors cause attenuation and degradation. Attenuation is, “The process by which all signal components decline equally in intensity due primarily to spherical spread,” whereas degradation is, “The destruction of signal structure as a result of reverberation, amplitude fluctuations, and differential attenuation at different frequencies” (definitions taken from Rabin *et al.* 2003). Oftentimes, animals must communicate in a noisy environment, consisting of noise from both conspecifics and heterospecifics. The creates what is known as the “Cocktail Party Problem” (Cherry 1953), due to masking of signals by noise. Noise interferes with the transmission, detection, and processing of communicative signals (Zhao *et al.* 2017). In the dusk chorus of insects, many families are calling in the same place, at the same time, and a masking effect may occur (Barber *et al.* 2010). Noise masking occurs when airborne noise inhibits the perception of sounds (signals or cues) relevant to animals. In communication, which is defined as an exchange of information between a sender and a receiver that benefit both parties, the sender-receiver dyad can change behaviors to compensate for noise interference. Senders can use spatial partitioning to make use of natural attenuation, as seen in crickets and katydids (Schmidt *et al.* 2013, Jain *et al.* 2014). This can occur horizontally or vertically, with insects climbing to different levels of the forest canopy to call (Diwakar and Balakrishnan 2007). The ground level is the often the most inefficient layer for sound propagation, while the mid-understory may be more optimal. Further, low foliage density reduces sound interference, while height above the ground reduces the effects of boundary waves (Schmidt and Balakrishnan 2014), leading to enhanced signal propagation. Animals may also alter attributes of their calls to overcome masking. This has been seen in birds, cetaceans, and

insects (Barber *et al.* 2010, Erbe and Farmer 2000, Thomas *et al.* 1990, Au *et al.* 2009, Morisaka *et al.* 2005, Schmidt and Balakrishnan 2014). An example of this is spectral partitioning, which occurs when a sender's signal has a spectral structure that minimizes frequency overlap with other signals and/or noise (Schmidt and Balakrishnan 2014, Hartbauer and Römer 2014). This is less practical in animals with broadband calls, but more so in those with a narrow frequency band in their calls, such as crickets (Riede 1993). Birds have been observed altering the frequency of their calls to overcome anthropogenic sources of noise such as urban traffic (Francis *et al.* 2009, Francis and Barber 2013, Shannon *et al.* 2016, Barber *et al.* 2010). Tree swallow chicks, *Tachycineta bicolor*, alter their begging calls in noise as well (Leonard and Horn 2008). Altering calls to overcome masking has also been seen in cotton-top tamarin (*Saguinus Oedipus*) contact calls (Egnor *et al.* 2007), and the alarm calls of squirrels (Rabin *et al.* 2006). Hypothetically, temporal partitioning could occur if senders use lead-lag call strategy and call at different times to avoid overlap. While examples of temporal partitioning have been reported in Amazonian parrots (Luther 2008), more research is needed to understand the conditions that lead to this signaling strategy.

Receivers must also be able to detect, localize and process the information in an acoustic signal, and thus in practical terms noise is a receiver psychology problem. Frequency tuning is one strategy for this problem and occurs when a receiver's auditory sensitivity matches the call of the sender, and all other frequencies are effectively tuned out, improving the signal-to-noise ratio (Capranica and Moffat 1983, Wehner 1987, Simmons 2013). Receivers can also exhibit spatial partitioning by moving to a location that minimizes the local effects of noise. This is known as spatial release from masking and has been recorded in crickets (Schmidt and Römer 2011) and katydids (Römer and Krusch 2000). In some animal systems, the sensory system

amplifies a relevant signal while attenuating non-focal sound in a process known as gain control (Pollack 1988). Constant noise, such as the trilling calls of katydids, can fade into the background, and receivers use novelty detection to recognize a salient signal from the background noise. This behavior is exhibited in a chirping species of katydid, whose signal timing (onset/offset timing) is detected above the constant trill of another local katydid species (Siegert *et al.* 2013). By altering their behavior to overcome noise masking of both signals and cues, animals have evolved a variety of solutions to deal with a noisy environment.

Effects of Noise on Circadian Rhythms and Daily Activity

When noise acts as a stressor or distraction, animals may shift their activities temporally to avoid the disturbance. Red foxes, *Vulpes vulpes*, cross roads more often at night (after midnight), when car traffic is lower. Here, the sound of cars indicates danger (risk of injury or death), and the red foxes alter their daily activities to avoid this danger (Baker *et al.* 2007). Harbor porpoises, *Phocoena phocoena*, actively avoided a noisy pool when given the choice to do so (Kok *et al.* 2018), and Minke whales and pilot whales have been observed to avoid areas with sonar (Kvadsheimet *et al.* 2017, Antunes *et al.* 2014). However, foraging opportunities can be reduced if an animal actively avoids areas with noise. In manatees, *Trichechus manatus latirostris*, daily feeding patterns changed in response to ambient noise (snapping shrimp and boat noise). Miksis-Olds *et al.* (2007) found that manatees utilize grass beds with less ambient noise from boats in the morning, indicating that the animals are selecting preferred habitat based upon the ambient noisescapes. In laboratory mice, *Mus musculus*, sensitivity to noise changes throughout the day, and the cochlea contains a self-sustained circadian clock that regulates this differential sensitivity to noise (Meltser *et al.* 2014). Laboratory mice are often more vulnerable when exposed to noise at night, and the circadian clock can even be dysregulated by exposure to

noise (Park *et al.* 2016). Additional research is required to understand the breadth and magnitude of noise effects on circadian patterns in animals.

Effects of Noise on Courtship Behavior

Changes in courtship behavior in response to ambient noise may produce the greatest costs to an animal's reproductive fitness, as opportunities to mate may be reduced or missed when avoiding noise or having signals masked, unless animals find a way to adjust courtship signals or signaling behavior in adaptive ways. This is widespread in birds. European robins, *Erithacus rubecula*, sing at night in areas that are noisy during the day, and show a diel pattern of communication that takes advantage of temporal fluctuations in anthropogenic noise (Fuller *et al* 2007). Some bird species show a remarkable ability to adapt to urbanization and its noise-related stressful conditions (Chace and Walsh 2006). These noise-resistant urban species often exhibit local adaptation to or behavioral plasticity in response to urban noise. House sparrows and starlings call earlier in the morning to avoid the morning rush-hour traffic noise (Arroyo-Solis *et al.* 2013). In the tropical cricket *Anurogryllus muticus*, calling males were shown to use the walls of houses in an urban setting to increase the amplitude of their calls (Erregger and Schmidt 2018). While there have been a few studies on how insects respond to urban noise conditions, additional research is required to understand if other species of insects dwelling in urban settings exhibit equally nimble solutions to the ubiquitous problem of noise.

Importance of Invertebrate Models

Studies on the effects of noise on invertebrates, particularly insects, are rather limited. From an ecological perspective related to their important role across trophic levels, understanding how noise influences insect behavior and fitness represents a critical need. The ability to detect sound has evolved multiple times in insects, resulting in an array of auditory

structures that can be found in almost any segment of the body (Morley *et al.* 2014). Insects may be the first animals to use airborne sound for long distance communication (Senter 2009) and do so mainly to attract mates (Gerhardt and Huber 2002). Their calls have been shaped over time by selection pressures, physical and physiological constraints, phylogenetic history, eavesdropping pressures, sexual selection, and biotic and abiotic factors in the environment (Endler 1993, Ryan 1990), not the least of which is noise constraints.

Vibrational communication is seen in many insect orders (an extensive look into 16 different groups is presented in Shestakov 2015) and was likely the communication modality that was the precursor to airborne signaling (Virant-Doberlet and Cokl 2004, Coccoft and Rodriguez 2005). Whereas airborne sound travels through the air as a medium, vibrational sound travels using the substrate as a medium. Male olive fruit flies, *Bactrocera oleae*, vibrate their wings to attract mates, while another species, *Anastrepha suspensa*, also vibrates its wings in territorial disputes (Benelli *et al.* 2012). Vibrational signals are also used for courtship in the stonefly suborder Arctoperlaria (Boumans and Johnsen 2015). Vibrational communication is also used in parent-offspring communication. In the treehopper, *Umbonia crassicornis*, a cluster of offspring produce a collective vibrational signal, which is transmitted through the plant stem, to warn their mother of an impending predator attack (Hamel and Coccoft 2012). Vibrational signals can be quite complex. The grasshopper, *Tetrix ceperui*, produces individual pulses and groups of pulses in male competition, post copulation, and copulation behavior (Kočárek 2010). The sensory structures that detect vibration signals are likely highly sensitive to substrate-borne vibrational noise (Shestakov 2015, Rajaraman *et al.* 2015, Gemeno *et al.* 2015). While insects have a suite of strategies to overcome natural biotic noise, including horizontal and vertical stratification, temporal partitioning, and spectral partitioning (Schmidt and Balakrishnan 2014, Brunnhofer *et*

al. 2016), it is not clear if these solutions are effective at offsetting the effects of substrate-borne vibrational noise. Burying beetle (*Nicrophorus marginatus*) parents were observed to take longer to bury a carcass and produced smaller broods when reproducing in conditions of seismic noise (Phillips *et al.* 2020). It is reasonable to assume that insects exhibit rapid evolutionary response to human-induced substrate-borne noise sources, but the literature remains relatively depauperate on this topic.

Crickets as a Model Organism

Crickets are a widely studied insect group that produce acoustic signals for pair formation and mating. Male crickets produce two calls: one for long distance mate attraction, and another, close range call for courtship after physical contact has occurred (Harrison *et al.* 2013, Rebar *et al.* 2009). Crickets stridulate to produce sound; in cricket stridulation a scraper, also known as a *plectrum*, is located on the dorsal side of one wing, and this is rubbed against a file, also called *stridens*, which is located on the ventral side of the other wing. Both the *plectrum* and the *stridens* can be found on each wing in crickets, and males usually use the left *plectrum* to excite the right *stridens* (Gerhardt and Huber 2002). Accurate reception of these signals is especially important for pair formation and copulation, as females will only mount males after they have localized the male and responded to his courtship call (Nelson and Nolen 1997). House crickets, *Acheta domesticus*, have been extensively studied in the field of communication and sensory biology. Although the importance of song in female choice has been studied in *A. domesticus* (Rek 2012, Stoffer and Walker 2012, Crankshaw 1979, Walikonis *et al.* 1991, Gray 1997, Gray 1999, Nelson and Nolan 1997, Stout and McGhee 1988), the effects of noise (iso-, cross-, and multimodal) on daily locomotion and male calling patterns has not been previously studied. Because noise has been shown to alter daily activities in animals (Baker *et al.* 2007, Kok *et al.*

2018, Kvadsheimet *et al.* 2017, Antunes *et al.* 2014, Miksis-Olds *et al.* 2007, Meltser *et al.* 2014, Park *et al.* 2016), it is reasonable to assume that *A. domesticus* may exhibit changes in daily patterns of locomotion when exposed to noise. Noise has also been documented as having masking and distraction effects (Francis and Barber 2013) on acoustically signaling species. *A. domesticus* males may avoid calling when noise is present; no study has definitively described this, however. Given the importance of the male call in facilitating mating for *A. domesticus*, the accurate transmission of the advertisement signal to the receiver target is directly linked to fitness outcomes. How males react to noise while calling may be key in understanding how they, and other animal species, respond behaviorally to novel anthropogenic noise sources that cross sensory system boundaries.

In the following two chapters I describe experiments that address two questions related to how and to what extent insect daily activity patterns and sexual signaling behavior is influenced by noise. In chapter 1, entitled “Behavioral response to multi-channel environmental noise: tracking noise-induced changes in daily locomotor patterns in the house cricket, *Acheta domesticus*,” crickets were exposed to noise in three forms: isomodal (airborne noise), crossmodal (substrate-borne vibration), and multimodal (airborne noise and substrate-borne vibration combined) and tracked in an activity monitor to assess to how and to what degree noise effects locomotion. Noise was presented both intermittently and continuously to determine if different exposure patterns would produce different behavioral effects, as crickets may be able to acclimate to noisy conditions. Different noise forms (airborne versus substrate-borne) may also have different effects, as separate sensory systems elements are utilized to perceive each.

In chapter 2, entitled “Behavioral response to multi-channel environmental noise: tracking noise-induced changes in male calling patterns in the house cricket, *Acheta domesticus*,

male crickets were exposed to the same three forms of noise, and recorded to assess to what degree noise affects male calling behavior. Noise exposure occurred both intermittently and continuously to determine if they would have different effects, as male crickets may respond differently to exposure based upon its temporal dosage. As in the locomotor activity tracked in chapter 1, different noise forms may also have different effects due to the sensory system organization in cricket. Male calling is essential to *A. domesticus* courtship and copulation, so any alteration in calling patterns in response to noise may have detrimental effects on reproduction.

CHAPTER 1: BEHAVIORAL RESPONSE TO MULTI-CHANNEL ENVIRONMENTAL NOISE: TRACKING NOISE-INDUCED CHANGES IN DAILY LOCOMOTOR PATTERNS IN THE HOUSE CRICKET, *ACHETA DOMESTICUS*

Introduction

Noise is often a byproduct of human activities, geophysical processes, and natural systems. While animal populations generally adapt to natural sources of noise, human-generated sources often pose challenges due to their relatively recent emergence across natural landscapes. Anthropogenic noise is both prevalent and complex, and interacts with multiple sensory modalities (Barber *et al.* 2010, Kight and Swaddle 2011, Luo *et al.* 2015). In some cases, hearing impairment and deafness can occur from a single impulsive acoustic event above the pain threshold (a single explosion for example), damaging the cochlea or related neural structures (Barber *et al.* 2010, Kight and Swaddle 2011, Rabin *et al.* 2003). Other physiological effects that are associated with more chronic noise exposure include shifts in neuronal structure (observed in laboratory rats, *Rattus norvegicus*, in Cui *et al.* 2009), heart damage (observed in laboratory mice, *Mus musculus*, in Gesi *et al.* 2002), developmental instability (also observed in laboratory rats in Møller and Swaddle 1998), and an increase in stress hormone production (observed in humans in Babisch 2003).

Animal activity levels are affected by noise exposure, and both short and long-term behavioral changes have been observed in taxa occupying sites with robust noisescapes. Animals may in some cases perceive noise as a distraction, an irritant, or as a potential source of danger (Luo *et al.* 2015, Rabin *et al.* 2003, Francis and Barber 2013). Animals may avoid habitats with noise all together; there are numerous examples of lower animal population levels near sources on anthropogenic noise (Barber *et al.* 2010, Proppe *et al.* 2013). Marsh frogs, *Pelophylax*

ridibundus, showed reduced locomotion in the presence of actual traffic noise during field experiments and artificial traffic noise in laboratory experiments (Lukanov *et al.* 2014). Captive harbor porpoises, *Phocoena phocoena*, preferred to avoid a noisy pool when given the option to move to a quiet pool (Kok *et al.* 2018). Similarly, Minke whales and pilot whales avoid areas with high levels of sonar (Kvadsheim *et al.* 2017, Antunes *et al.* 2014). Animals may shift their activities to times of day when noise acts as a distraction or irritant. Manatees, *Trichechus manatus latirostris*, exhibit changes in daily feeding in response to ambient noise (snapping shrimp and boat noise). Miksis-Olds *et al.* (2009) found that manatees utilize grass beds with less ambient noise in the morning, when boats are more active. Red foxes, *Vulpes vulpes*, cross roads more often at night (after midnight), when car traffic is lower. Here, the sound of cars indicates danger (Risk of injury or death), and red foxes alter their movements to lower their risk of being injured (Baker *et al.* 2007). A possible consequence of these changes in daily activity is that foraging opportunities may be missed (Brown *et al.* 1999). In laboratory mice (*Mus musculus*), sensitivity to noise changes throughout the day, with the cochlea containing a self-sustained circadian clock that regulates this differential sensitivity to noise (Meltser *et al.* 2014). This results in a greater impact of noise at night, when mice are more active.

Noise is complex, and can be transmitted through air, water and solid substrates, or even through multiple substances at once. Isomodal noise occurs in a single sensory modality, and interferes with communication in the same modality as a transmitted signal. For example, airborne traffic noise is known to mask parent-offspring acoustic communication in the blue tit, *Cyanistes caeruleus* (Lucass *et al.* 2016). Noise can also be found in the context of and interacting with other sensory channels. For example, acoustic noise can interfere with visual, chemical, and vibrational signals, thus causing crossmodal interference (Vandersal and Hebets

2007, Halfwerk and Slabbekoorn 2015). Noise can also be multimodal, interacting with multiple sensory channels at once (sound, visual, chemical, vibration). Anthropogenic noise often exhibits this multimodal complexity, and thus holds potential to influence animal behavior as a multisensory pollutant (Halfwerk and Slabbekoorn 2015).

Most studies on noise effects on animals have been focused on vertebrate species, particularly avians and marine mammals (Shannon *et al.* 2016, Francis and Barber 2013), but far less attention has been paid to invertebrates, which account for 80% of the biomass on the planet (Lewbart 2006). Many invertebrates, especially arthropods, have sensory systems that are highly sensitive to ambient noise, and many groups have evolved novel adaptations for foraging and locating mates in biotically noisy conditions (Morley *et al.* 2014). In the dusk chorus of insects for example, many groups are calling in the same place, at the same time, and a masking effect may occur (Barber *et al.* 2010). Masking occurs when noise inhibits the perception of signals or cues relevant to animals. Signalers may offset this effect via spatial portioning, spacing themselves to make use of natural sound attenuation, as observed in some crickets and katydids (Schmidt *et al.* 2013, Jain *et al.* 2014). Spatial portioning can occur in either a horizontal or vertical plane, with insects occupying different levels of a forest or scrub canopy to call (Diwakar and Balakrishnan 2007). Insects also exhibit adaptive features of their acoustic calls that contribute to lowered risk of masking. Spectral partitioning is a good example of this form of adaptation, which occurs when a sender's signal has a spectral structure that minimizes frequency overlap with other signals and/or noise (Schmidt and Balakrishnan 2014, Hartbauer and Römer 2014). This is adaptive solution is less practical for signalers with broadband calls, but more so for those with an intrinsically narrow call frequency, such as crickets (Riede 1993). Alternatively, the narrow-band nature of the cricket call itself may in part be the result of

selection for spectral segregation, in addition to morphological constraints of the sound production mechanisms.

Sound producing insects in the order Orthoptera, such as the true crickets, are especially sensitive to airborne sound and substrate-borne vibration due to their reliance on signals and cues in these modalities (Huber *et al.* 1989). Cricket biology related to sound production and reception, pair formation and mating, and sensitivity to substrate-borne vibration in the context of conspecific and heterospecific interactions are well studied (Howard *et al.* 2008, Howard *et al.* 2018, Bentley and Hoy 1974, Hedwig 2006, Pollack 2015, Moiseff *et al.* 1978). Crickets can detect airborne pressure waves, near-field particle motion, and substrate-borne vibration, making them in effect natural noise sensors. House crickets, *Acheta domesticus*, pay attention to sound and vibration in the dual context of mating and predation avoidance. Although the importance of sound in the context of female phonotaxis has been well studied in *A. domesticus* (Rek 2012, Stoffer and Walker 2012, Crankshaw 1979, Walikonis *et al.* 1991, Gray 1997, Gray 1999, Nelson and Nolan 1997, Stout and McGhee 1988), the effects of noise (iso-, cross-, and multimodal) on daily activity patterns has not been previously examined. Measuring how these fine-scale diel locomotor patterns, which are tightly linked to metabolic budgets, are altered in the presence of noise sources that cross sensory system boundaries may get us closer to understanding more accurately the true fitness cost of noise.

The purpose of this study was to determine if different forms of noise have an effect on the daily locomotor patterns of the house cricket, *Acheta domesticus*. Using automated locomotion monitors and experimental noise playback experiments, I ask the following questions: 1. Does exposure to isomodal (airborne), crossmodal (substrate-borne vibration), and/or multimodal (both airborne and substrate-borne) noise alter daily activity patterns in

Acheta domesticus when presented intermittently during peak hours of natural activity? I hypothesized that exposure to noise during the peak activity period (intermittent noise) would alter the temporal structure and magnitude of activity in adult house crickets. Due to the effects of signal masking, behavioral disruption, and interference with eavesdropping on airborne predators, I predicted that exposure to intermittent isomodal noise (airborne) during periods of peak activity would result in lowered locomotor activity in these peak periods and increased locomotor activity during typically quiescent periods, with the overall volume of activity remaining unchanged in comparison to controls. I also predicted that due to sensory interface with the subgenual organ, which is involved with terrestrial predator detection and the resulting flight response, exposure to intermittent crossmodal noise (substrate-borne vibration) during periods of peak activity would result in lowered locomotor activity in these peak periods and increased locomotor activity during typically quiescent periods. Due to the high stakes associated with predation avoidance behavior, I predicted that the overall effect of substrate-borne noise would be greater than that of isomodal noise alone, and the overall volume of activity would be greater than measured in control trials. I also predicted that due to sensory interface with both the subgenual and auditory organs, which is involved in both conspecific signal and predator detection, exposure to intermittent multimodal noise (airborne and substrate-borne vibration) during periods of peak activity would result in lowered locomotor activity in these peak periods and increased locomotor activity during typically quiescent periods. I predicted that the effect on behavior of multimodal noise would be greater than that of either isomodal or crossmodal noise alone, and the overall volume of activity greater than measured in control trials. 2. Does exposure to any of the three aforementioned noise types alter daily activity patterns in *Acheta domesticus* when presented continuously? I hypothesized that exposure to continuous noise

would alter the overall volume of daily activity in adult house crickets, with variable effects on the temporal patterns of activity. Due to the effects of signal masking, behavioral disruption, and interference with eavesdropping on airborne predators, I predicted that exposure to continuous isomodal noise (airborne) would result in an overall decrease in daily locomotion activity in *A. domesticus* compared to control trials, with the temporal pattern of activity across the 24-hour period measured remaining unchanged. I also predicted that due to sensory interactions with the subgenual organ, which is involved with terrestrial predator detection and the resulting flight response, that exposure to continuous crossmodal noise (substrate-borne vibration) would result in an overall increase in daily locomotion activity in *A. domesticus* compared to control trials, with the overall temporal pattern of activity disrupted across the 24-hour measurement period. I also predicted that due to sensory interference with both the subgenual and auditory organs, which are involved in both conspecific signal and predator detection, exposure to continuous multimodal noise (airborne and substrate-borne vibration) would result in an overall increase in daily locomotion activity in *A. domesticus* compared to control trials, with the effect greater than that of crossmodal noise alone. Similar to continuous substrate-borne noise, I expected that multimodal noise would lead to disruption of the overall temporal pattern of activity across the 24-hour period measured.

In summary, I hypothesize that response to noise in house crickets will scale in magnitude with noise complexity and relationship to ecological relevance. Accordingly, I expect that multimodal noise will produce the greatest effect on daily activity patterns, and isomodal the least. Additionally, I expect that continuous noise will produce a larger effect on daily activity patterns than intermittent noise conditions, across all three noise types.

Methods

Animals

Penultimate instar *A. domesticus* nymphs were obtained from Fluker Farms® (Port Allen, LA) and separated by sex upon arrival to ensure virginity upon eclosure as adults. Crickets were housed in the Integrative Animal Behavior Laboratory at the University of New Hampshire, Durham in an insectarium space maintained at 23° Celsius and 46% relative humidity, with a 14:10 light/dark cycle to mimic the seasonality of summertime reproduction (lights on from 06:00-20:00, and lights off 20:00-06:00). Crickets were fed Meow Mix® original choice cat food, ground into a course powder (30% crude protein, 11% crude fat, 4% crude fiber, 12% moisture) and provided paper towels soaked in bottled drinking water *ad libitum*. They were housed in 37.85 liter glass aquaria with mesh screen tops and either egg crate or paper towel/toilet paper rolls for a substrate and refugia. Cricket culture density was maintained at approximately 6.6 crickets per liter⁻¹. Different individuals were used for each trial.

Controls

To establish daily locomotor activity patterns in *A. domesticus*, an initial control trial was conducted with fifty reproductively mature crickets (31 males and 24 females). Crickets were placed into individual cells of a locomotor activity monitor (LAM; TriKinetics Inc. Waltham, MA), monitored using TriKinetics DAMsoftware ran on a Lenovo X250 (MS Windows ver. 7 Professional) laptop. The monitor (Figure 1a) consisted of 32 transparent Lexan tubes (2.5 cm wide x 8.0 cm long) sealed with fine aluminum mesh screening at one end, and a solid plastic cap at the other. Each tube is positioned such that a photoeye array in the LAM (Figure 1b) with six sensors records movement as the cricket breaks the photo eye array. Each time this occurs it is recorded as a discrete “event,” with event data collected continuously and binned by the

minute, as in Chiu *et al.* (2010). A single cricket was placed in each LAM tube and provided with food and water on opposite ends of the prep, and locomotor activity was recorded continuously over the course of five days. Trials occurred inside of a semi-anechoic chamber with internal temperature maintained at 23 C, with a 14:10 L:D photoperiod. The first 24 hours of each trial served as an acclimation period to account for enclosure effects. Activity counts from the four days following the one day acclimation period were binned by the hour using TriKinetics FilesScan software, and then aggregated into two-hour time blocks in Microsoft Excel. Time blocks were identified as follows: time block 1= 06:00-08:00, time block 2= 08:00-10:00, time block 3= 10:00-12:00, time block 4= 12:00-14:00, time block 5= 14:00-16:00, time block 6= 16:00-18:00, time block 7= 18:00-20:00, time block 8= 20:00-22:00, time block 9= 22:00-24:00, time block 10= 24:00-02:00, time block 11= 02:00-04:00, and time block 12= 04:00-06:00. We identified peak activity periods by testing for differences in activity counts across the 12 time blocks using a Kruskal-Wallis test in JMP version 13.0, followed with a post hoc Dunn's test for joint rankings to evaluate inter-block differences. We used the identified peak locomotor activity period as the presentation window for subsequent noise treatments (isomodal airborne noise, crossmodal substrate borne vibration, and a combination of both for a multimodal noise stimulus) in intermittent noise trials.

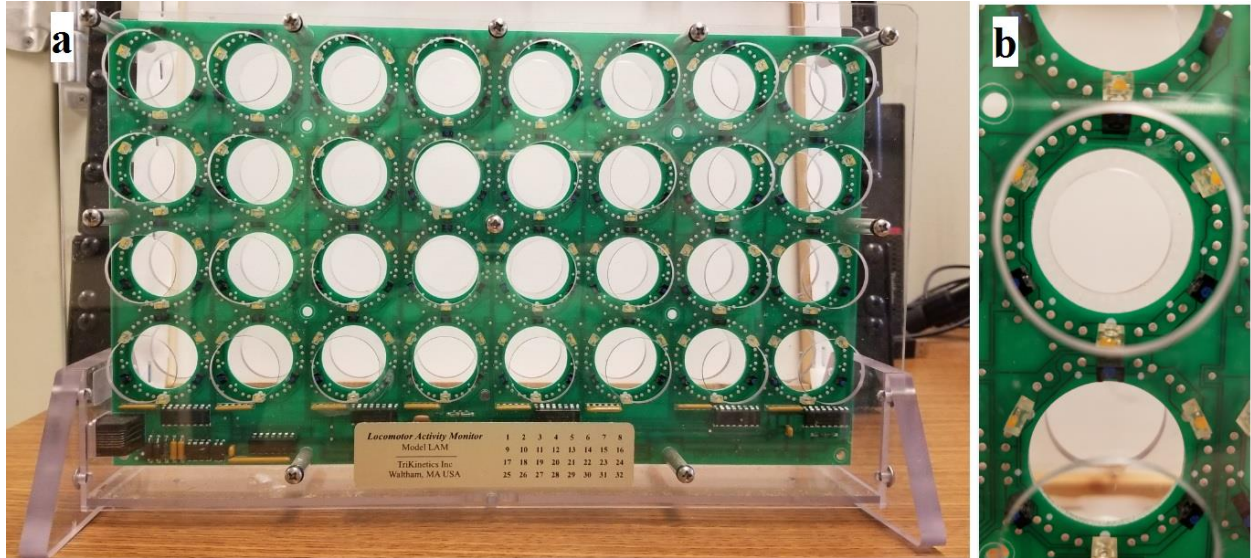


Figure 1: The TriKinetics locomotor activity monitor. The monitor (a) consists of 32 slots for supporting transparent Lexan tubes. Each tube contained one cricket, and the photo eye array (b) counted each time the cricket walked through the photoeye beam of the sensors.

Isomodal Noise Exposure

The airborne noise stimulus used for isomodal and multimodal noise was a 500 ms pulse train of white noise (energy concentrated evenly between 20Hz-22050Hz) with 5-sec inter-pulse intervals played for the duration of the 2-hour peak activity period in intermittent noise trials.

The 16 bit sound file was created in Adobe Audition version 3.0, generated with a sample rate of 44.1 KHz, and corrected for intrinsic speaker distortion using a custom script in Matlab (ver.

2017b, MathWorks, Natick, MA). Noise was presented from two electromagnetic speakers (Orb

Audio Mod-1 25-watt) positioned 45.0 cm in front of the LAM preparation, and calibrated for

amplitude (85.0 decibels SPL) prior to trials using a Brüel and Kjær G-4 2250 Lite sound

pressure meter (C weighted averages). The microphone for the sound pressure meter was

attached to 3.0 m extension cable to measure sound pressure from the midpoint of each activity

tube. As in the controls, each treatment lasted five days, with the first day being used as an

acclimation period. For intermittent noise exposure trials, the stimulus was presented only during

the previously determined peak locomotor activity period over the course of the four post-

acclimatization days. For continuous noise trials, stimulus was played for the entire four-day period (24 hours per day), while simultaneously collecting cricket locomotor activity data. After binning one-minute activity event data into hour bins using Trikinetics FilesScan software, locomotor activity data was aggregated into two-hour bins in Microsoft Excel and analyzed using a Kruskal-Wallis test in JMP Pro version 13.0 to evaluate differences in activity counts across the time blocks, followed by a post-hoc Dunn's test for joint rankings to identify differences between time blocks.

Crossmodal Noise Exposure

The substrate-borne vibration stimulus used for crossmodal and multimodal noise treatments was a 60-second train of 500 ms vibration pulses (brown noise, generated and band pass filtered in Adobe Audition version 3.0 to generate most energy between 10-300 Hz) with 5-sec inter-pulse intervals that was used in looped playbacks during the specified presentation period. In treatments with substrate-borne noise (crossmodal and multimodal conditions), an electromagnetic shaker (AuraSound, Inc. AST-2B-04 50-Watt bass shaker) was bolted to the underside of a custom raised platform (61x18x13 cm) on the top of which was affixed the locomotor activity monitor used in all other trials (Figure 2). The shaker was powered by an ART SLA4 4-Channel 140 Watt amplifier (ART ProAudio, Niagara Falls, NY) and was calibrated before each trial with a Polytech PDV-100 laser Doppler vibrometer (Polytec GmbH, Waldbronn, Germany) to an amplitude of 15.0 mm/sec (9.4 m/s^2). As in all other trials, each treatment lasted five days, with the first day being used as an acclimation period. For intermittent noise trials, the stimulus was presented during the previously determined peak locomotor activity period over the course of the four noise exposure days. For continuous noise trials, the stimulus was played for the entire four-day period. After binning activity counts into hour bins using

Trikinetics FilesScan software, locomotor activity data was aggregated into two-hour bins in Microsoft Excel as above and analyzed using a Kruskal-Wallis test in JMP Pro version 13 to identify differences across the 12 time blocks, followed by a post-hoc Dunn's test for joint rankings to evaluate differences between time blocks.

Multimodal Noise Exposure

Multimodal noise treatments consisted of both airborne and substrate-borne stimuli parameterized and calibrated as in the isomodal and crossmodal trials, resented synchronously. Each multimodal treatment lasted five days, with the first day being used as an acclimation period. For intermittent multimodal noise trials, the combined airborne and substrate-borne noise stimulus was presented during the previously determined peak locomotor activity period over the course of the four noise exposure days. For continuous noise trials, the multimodal stimulus was played for the entire four-day period. After binning activity counts into hour bins using Trikinetics FilesScan software, locomotor activity data was aggregated into two-hour bins in Microsoft Excel as above and analyzed using a Kruskal-Wallis test in JMP Pro version 13 to identify differences across the 12 time blocks, followed by a post-hoc Dunn's test for joint rankings to evaluate differences between time blocks.

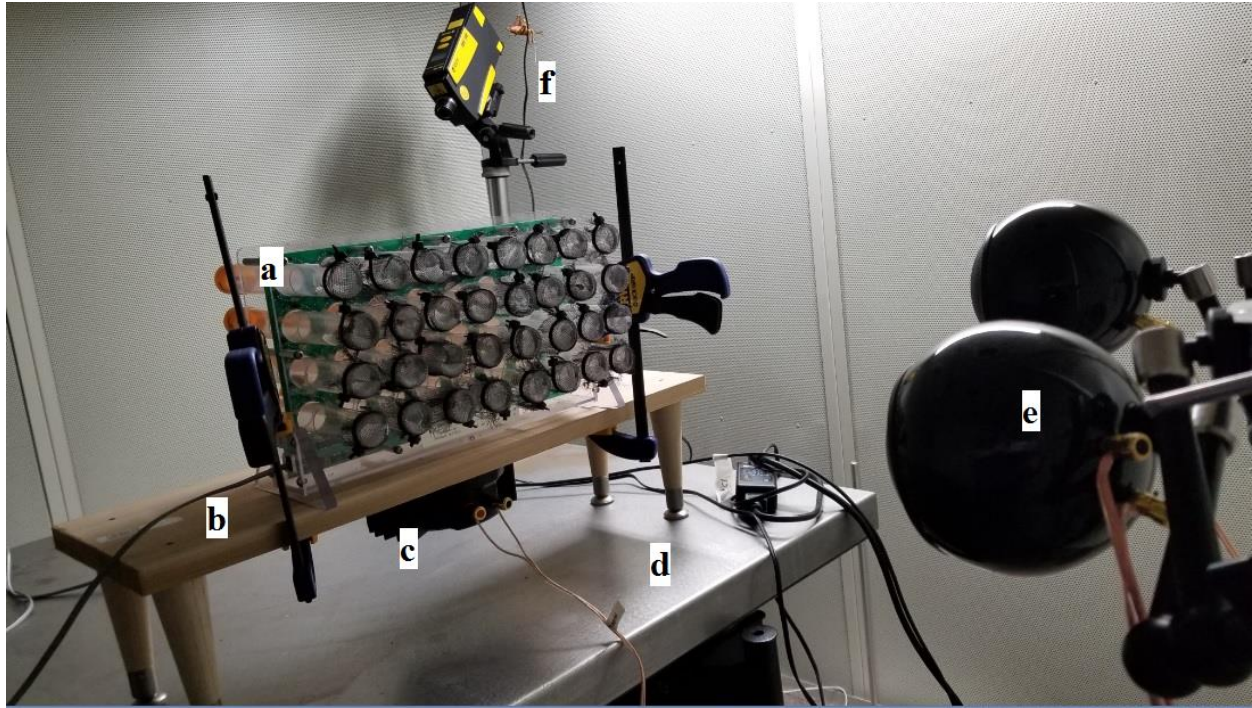


Figure 2: The experimental setup. The locomotor activity monitor (a) is seen with 32 tubes, each containing one cricket, with food and water on either side. One side is capped (orange plastic cap), while the other is covered with mesh screening to allow airborne noise to pass through. The monitor sits on a wooden platform (b) which contains the bass shaker underneath (c). The platform sits on a vibration isolation table (d) within the hemi-anechoic chamber. Two speakers (e) were used for airborne noise playback. A laser doppler vibrometer (f) was used to calibrate substrate vibration.

Results

Control

In control trials ($n=32$), I found that *Acheta domesticus* daily activity was concentrated during daylight hours and count totals were asymmetrically distributed across time blocks (Kruskal-Wallis 1-way test, χ^2 approximation, $X^2 = <0.0001$, $df = 11$, $P < 0.0001$), with peak locomotor activity during time blocks 4 and 5 (Figure 3; post hoc Dunn's Method for Joint Ranking $P < 0.05$). These two adjacent time blocks (12:00-16:00) thus served as the noise presentation period for subsequent intermittent stimulus trials (iso, cross, and multimodal).

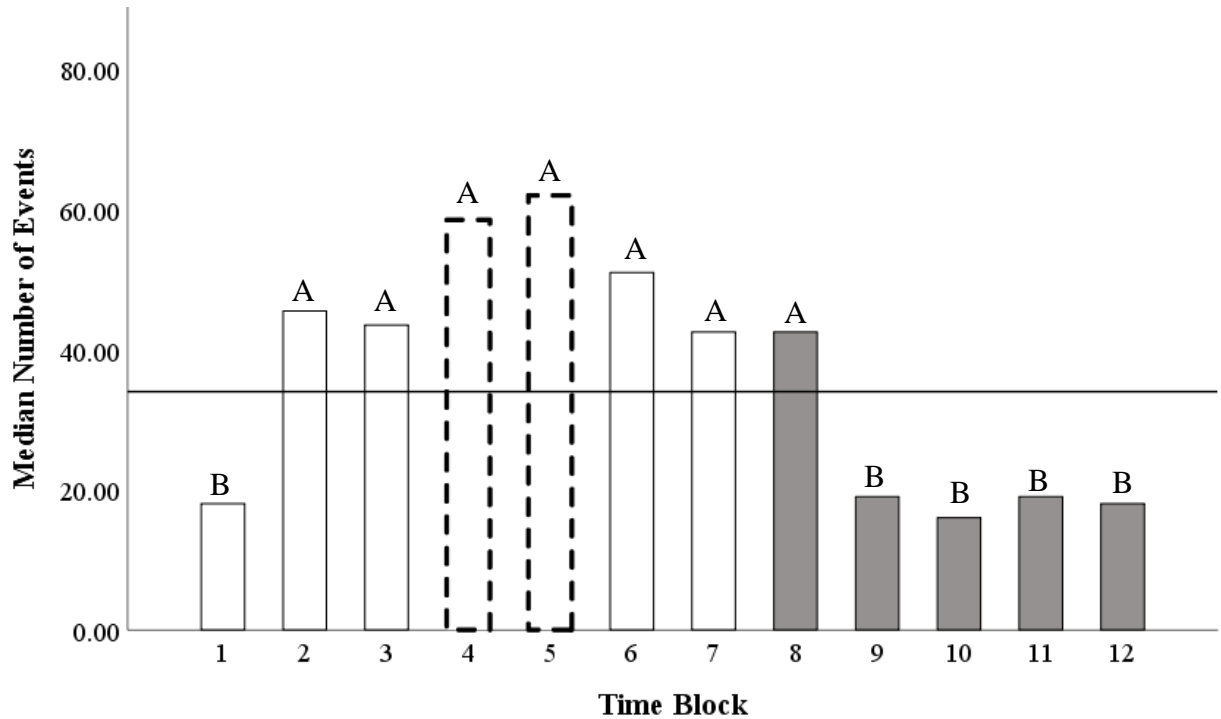


Figure 3: Median number of events per two-hour time block in control trials. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). The greatest number of locomotory events was observed during time blocks 4 and 5 (12:00-16:00) indicated with dashed lines. Activity was significantly higher in time blocks 2 through 8 (A), and lower in time blocks 9-12 and 1 (B). The Y-axis line indicates the median number of events for control conditions, irrespective of time block (34).

Isomodal Noise

Intermittent isomodal noise (airborne sound) trials (n=51) were conducted between 12:00 and 16:00 for four days. In response to noise treatments, the peak period of locomotor activity in *A. domesticus* shifted from time blocks 4 and 5 (12:00-14:00 and 14:00-16:00) to time block 2 (08:00-10:00) (See Figure 4, Kruskal-Wallis 1-way test, $\chi^2 = <0.0001$, $df = 11$, $P < 0.0001$; post hoc Dunn's Method for Joint Rankings $P < 0.0001$). The median number of events for block 2 increased from 63 to 77 in response to noise treatment, while locomotory events in time blocks 4 and 5 decreased to 40 and 30 from 60 and 63 events respectively.

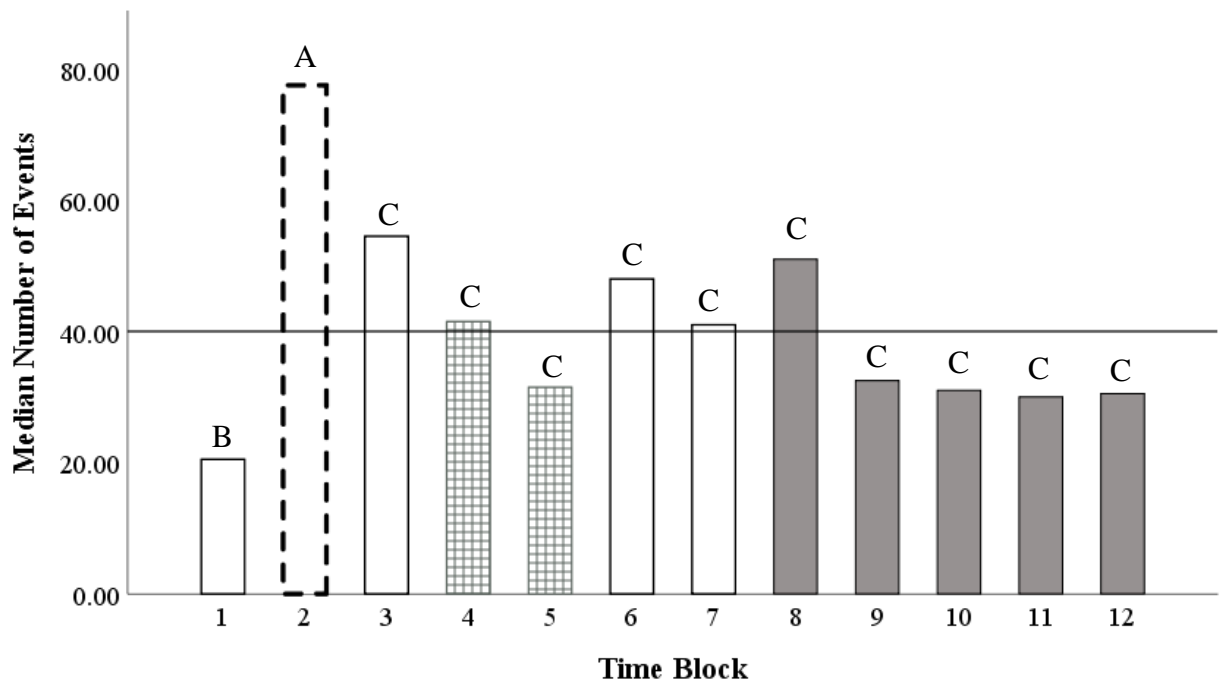


Figure 4: Median number of events per two-hour time block, intermittent isomodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). The peak number of events was seen in time block 2 (indicated with dashed lines), from 08:00-10:00. Airborne noise was played during time blocks 4 and 5 (12:00-14:00 and 14:00-16:00, indicated with grid pattern). These blocks had fewer events than in control conditions, and were no longer the peak periods. Time block 1 (B) had significantly lower events than most other time blocks. The Y-axis line indicates the median number of events with intermittent isomodal noise exposure, irrespective of time block (40).

Continuous isomodal noise (n=40) resulted in suppression of locomotor activity, with all time blocks having lower numbers of events than control conditions (Figure 5). Kruskal-Wallis test indicated that the number of events per time block were significantly different (χ^2 approximation $X^2 = <0.0001$, $df = 11$, $P < 0.0001$), though the Dunn method for joint rankings found few pairs that were significantly different. Time block 1 had a significantly lower number of events than others (A on Figure 5, Dunn method for joint rankings $P < 0.05$). Though time blocks 4 and 5 were still the highest in this treatment, the Dunn method found no significance.

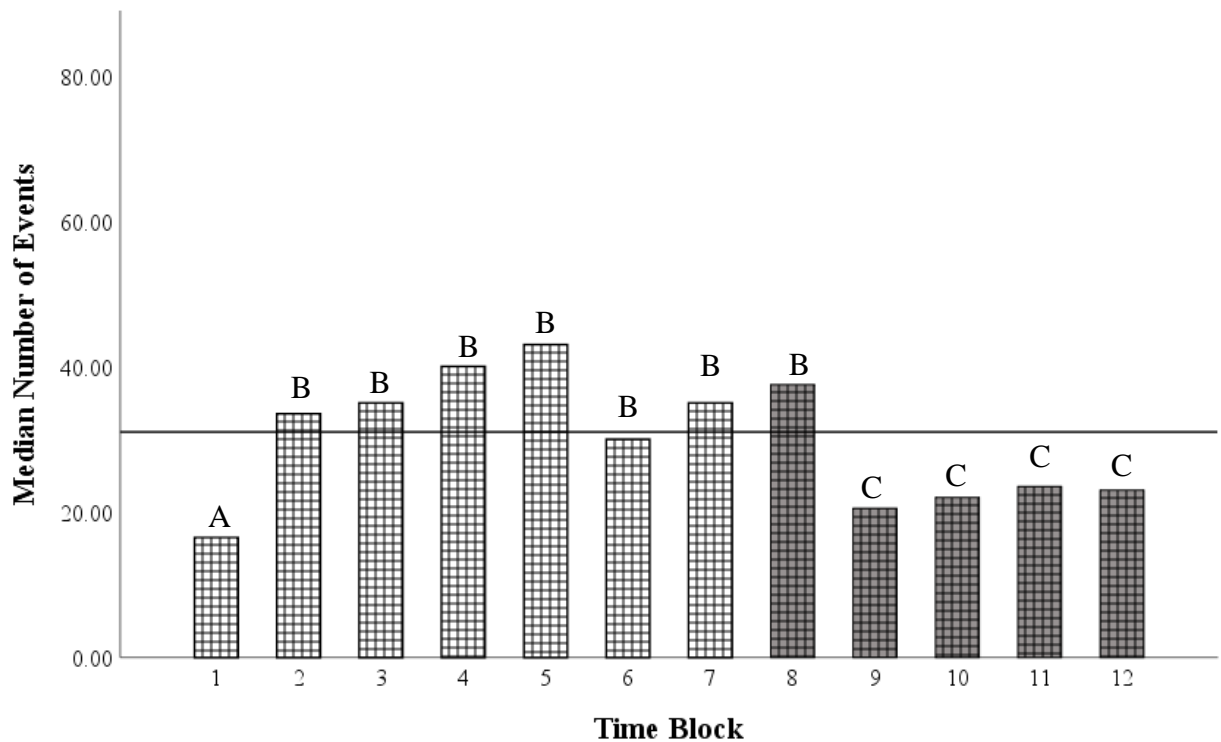


Figure 5: Median number of events per two-hour time block, continuous isomodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). The number of events in all time blocks was lower than control conditions. Time block 1 (A), from 06:00-08:00, was significantly lower than most other time blocks. There was no peak locomotor period. The Y-axis line indicates the median number of events with continuous isomodal noise exposure, irrespective of time block (31).

Crossmodal Noise

Exposure to intermittent crossmodal noise (substrate borne vibration, n=26) resulted in no significant differences between time blocks (Kruskal-Wallis 1-way test, χ^2 approximation $X^2 = 0.3370$, $df = 11$). The number of events per time block was similar to values in control conditions, and remained almost constant throughout the day, despite the appearance of time block 10 being lower than others (Figure 6). There was no statistically significant peak in locomotor activity.

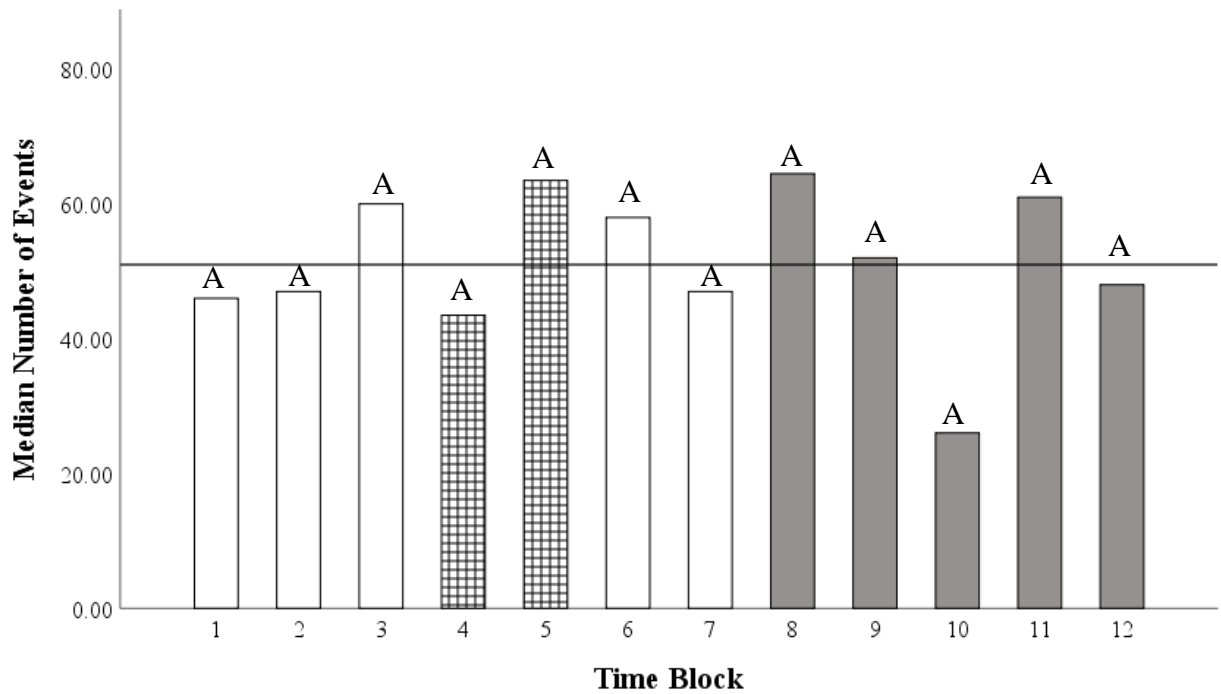


Figure 6: Median number of events per two-hour time block, intermittent crossmodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). Substrate vibration was produced for four hours during time blocks 4 and 5, indicated with a grid pattern. Time blocks were not significantly different from each other (Dunn method $p=0.3370$), despite the appearance of time block 10 being lower than all other time blocks. The number of events per time block differ from control conditions in terms of how crickets distributed activity throughout the day. The Y-axis line indicates the median number of events with intermittent crossmodal noise exposure, irrespective of time block (51).

With continuous crossmodal noise exposure ($n=30$), time block 1 (Figure 7, indicated by A, 06:00-08:00) was significantly lower than all other time blocks (Kruskal-Wallis 1-way test, χ^2 approximation $X^2 = <0.0001$, $df = 11$, $p < 0.0001$). Time block 3 had a higher number of events than others, though this was not a significant comparison (Dunn Method for Joint Rankings $P > 0.05$). Overall activity was slightly lower than control conditions.

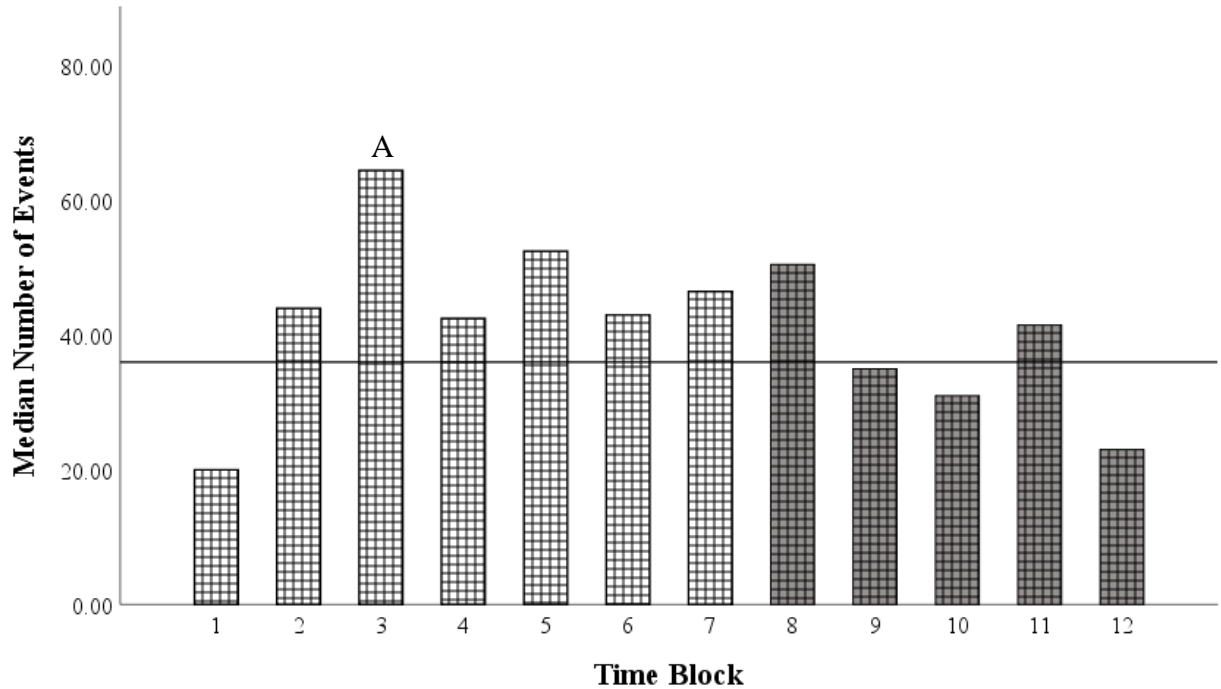


Figure 7: Median number of events per two-hour time block, continuous crossmodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). Time block 1 (A, 06:00-08:00) was significantly lower than all other time blocks (Dunn method $p < 0.05$). There was no statistically significant peak locomotor period. The Y-axis line indicates the median number of events with continuous crossmodal noise exposure, irrespective of time block (36).

Multimodal Noise

Intermittent multimodal noise exposure ($n=41$) shifted the peak locomotor period to time block 6, 16:00-18:00 (Kruskal-Wallis 1-way test, χ^2 approximation $X^2 = <0.0001$, $df = 11$, $P < 0.0001$), post hoc Dunn's Method for Joint Rankings $P < 0.05$, see Figure 8, indicated with dashed lines). This is later than peak locomotion in control conditions. The number of events per time block were larger than both control conditions (median values in the 60's for intermittent multimodal noise versus in the 30's in control conditions), and all other experimental conditions.

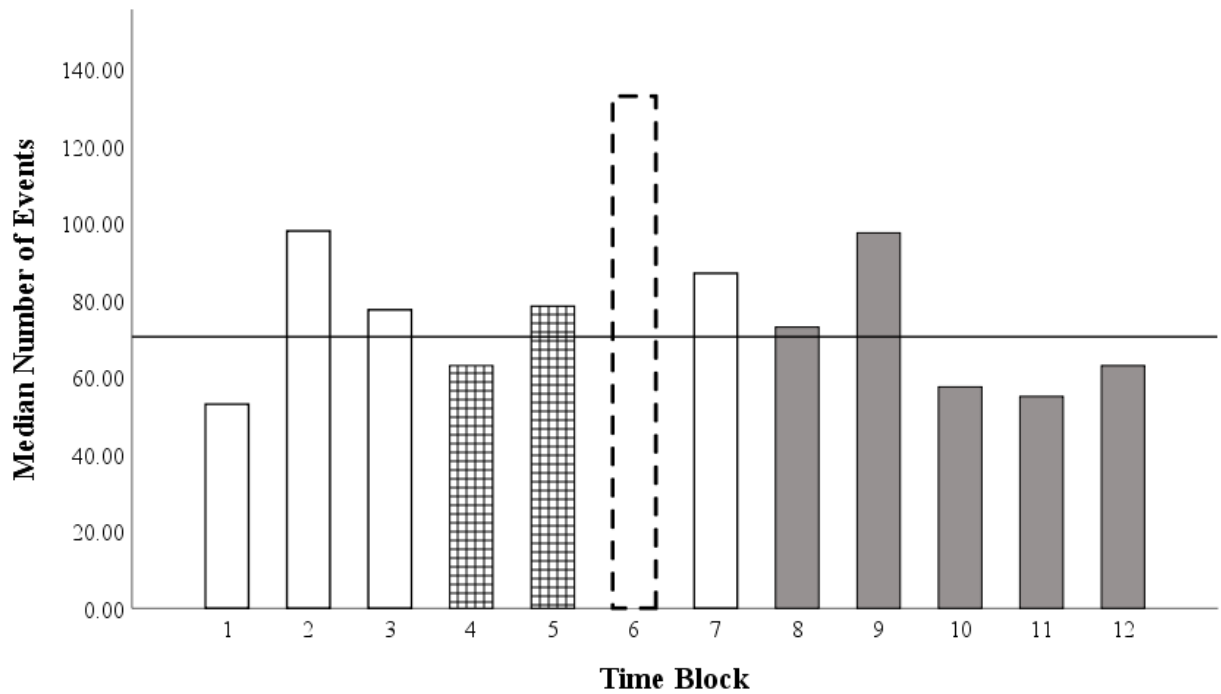


Figure 8: Median number of events per two-hour time block, intermittent multimodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). Airborne noise and substrate borne vibration were played for four hours during time blocks 4 and 5 (12:00-16:00, indicated with grid pattern). Note that the scale of these data has increased, with the peak events in time block 6 (dashed lines, 16:00-18:00) reaching 130 (Dunn method $p < 0.05$). The Y-axis line indicates the median number of events with intermittent multimodal noise exposure, irrespective of time block (70.5).

Continuous multimodal noise ($n=46$) resulted in suppresstion of locomotor activity (Figure 9). Median number of events across time blocks was 16, versus 34 in control conditions. There was no locomotor peak, and time blocks 1, 9, 10, 11, and 12 were all significantly lower than other time blocks (Kruskal-Wallis 1-way test, $\chi^2 = <0.0001$, $df = 11$, $p < 0.0001$, Dunn Method for Joint Rankings $P < 0.05$).

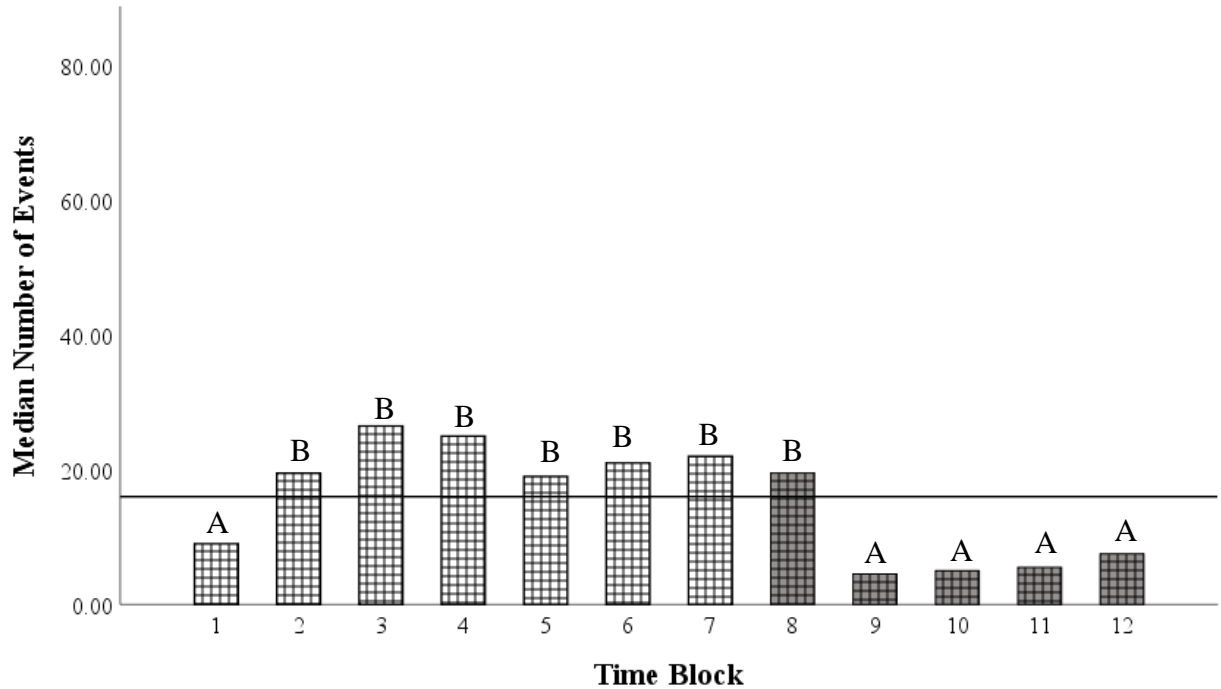


Figure 9: Median number of events per two-hour time block, continuous multimodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). Time blocks 1, 9, 10, 11, and 12 (A) were significantly lower than other time blocks (Dunn method $p < 0.05$). There was no peak locomotor period. The Y-axis line indicates the median number of events with continuous multimodal noise exposure, irrespective of time block (16).

When comparing all treatments together, the effect of multimodal noise exposure becomes more apparent (Figure 10). Here, we can see that multimodal treatments differ from controls in median event counts, and the two treatments have opposite effects. Intermittent multimodal noise exposure dramatically increased locomotion, while continuous multimodal noise dramatically decreased locomotion. Continuous sound exposure also produced a weakly significant effect (suppressing activity, like continuous multimodal exposure).

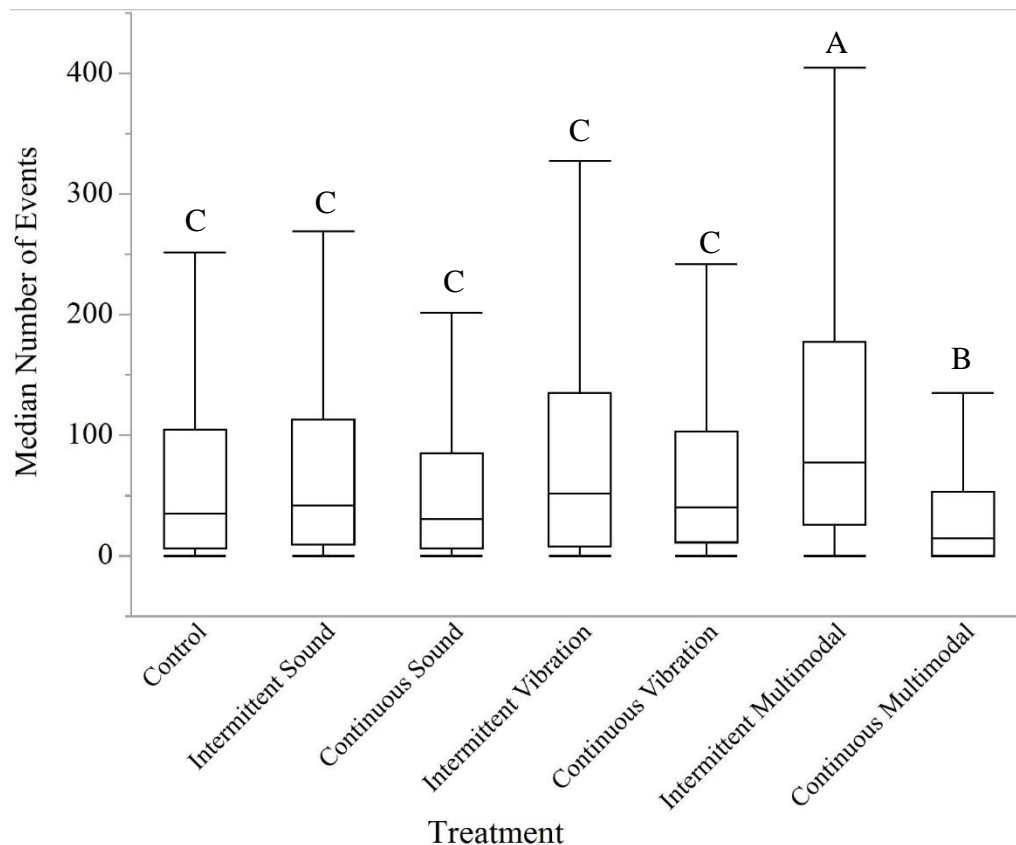


Figure 10: Median number of events per treatment. Multimodal trials produced the greatest difference from control conditions, but with opposite effects. Activity was increased with intermittent exposure, and decreased with continuous exposure.

Discussion

Data from this study provide support for diurnal locomotion in *Acheta domesticus*, with the majority of locomotor behavior observed between 12:00-16:00. Lutz (1932) found high activity during the first half of the night, whereas a study by Nowosielski and Patton (1963) found high individual variation in activity, but with activity peaks at the outset of dark periods. The study looked at adults and last larval instars and found that last larval instar crickets were less active than adults and had almost no temporal concentrated pattern of activity. Lutz (1932) found that in adults, some individuals had one peak of activity right after the onset of dark, and others exhibited a second peak of activity before dark. The authors note that not all crickets in the study fell into one category or the other, but that the pattern remained consistent after crickets

completed their final molt. The authors observed no difference in locomotor activity between the sexes, and reason that individual variation in activity is likely maintained as a mechanism to allow greater utilization of resources. My current findings document a peak locomotor period of 12:00-16:00, which falls within the second peak observed by Nowosielski and Patton (which started between 14:00 and 15:30), though no evening peak was observed in the current study. It should be noted that Nowosielski and Patton raised crickets under a different light cycle (12:12 08:00-20:00 versus 14:10 in the present study), and the authors noted that *A. domesticus* adults exhibit plasticity with respect to entrainment to differing L:D regimes.

With respect to activity patterns across time, all six noise treatments resulted in a change in daily locomotor activity compared to control trials. The largest pattern shifts were observed in treatments with continuous airborne noise (continuous isomodal noise and continuous multimodal noise), with *A. domesticus* exhibiting reduced locomotion in response to continuous airborne noise. This response was not observed in trials with intermittent airborne noise (intermittent isomodal noise and intermittent multimodal noise), but rather intermittent noise tended to cause significant shifts in locomotor peak times. This shift in activity moved peak locomotion prior to the noise exposure period in isomodal trials, and after noise exposure in multimodal trials. In contrast, continuous airborne noise caused *A. domesticus* to simply reduce investment in movement. This contrasts with a study conducted with zebrafish, *Danio rerio*, in which fish showed a startle response when exposed to irregular noise, which was stronger than the response to continuous noise (Sabet *et al.* 2015). Another study with harbor porpoise, *Phocoena phocoena*, also found a greater response to intermittent versus continuous noise in terms of avoidance behavior (Kok *et al.* 2018).

Crossmodal noise trials produced strikingly different results. In intermittent crossmodal noise trials, time blocks were not significantly different from each other; noise appears to have eliminated the activity peaks documented in controls. No peak was seen with continuous crossmodal noise exposure either. A statistically significant low period was found from 06:00-08:00, but this was seen in both control and other experimental trials. Both crossmodal noise trials had similar numbers of events to control conditions. Crickets sense vibration through their subgenual organs, which act as a first line of defense against predation. It appears that both forms of substrate-borne vibration elicited a behavioral response that resulted in the elimination of natural daytime activity peaks; this might simply represent an adaptive response in the face of perceived predatorial risk. When all treatments were compared to each other, multimodal noise exposure resulted in the greatest changes in locomotor activity when compared to control conditions. Because opposite effects were seen (increase in locomotion with intermittent exposure, and a suppression of locomotion with continuous exposure), it is reasonable to assume that *A. domesticus* react differently to this sensory pollution depending on the duration.

Overall, it is evident that multiple forms of noise had a significant effect on the locomotor behavior of *Acheta domesticus*, and each form of noise produced a different behavioral response. A suppression response can be seen with continuous airborne and continuous multimodal noise. Because the normal daily pattern of locomotion has been interrupted, it is possible that fitness consequences could be seen. If *A. domesticus* is experiencing a startle response by remain still more often with continuous noise, this could mean that less time is being spent on tasks crucial to survival, including foraging, finding shelter, or finding a mate. Noise changed the daily pattern of locomotion in all noise treatments, meaning that these consequences may be seen in conditions other than continuous iso- and multimodal noise. Remaining still could make *A.*

domesticus an easy target for predators, which may alter population levels and food chains long term. This is an important factor to consider when applying these findings to other species.

Because insects account for so much of the biomass on the planet, it is imperative to consider how our actions, including the noise we may produce, may affect them on a daily basis. Perhaps some species will be better at dealing with anthropogenic noise than others, but there is no way to know this without further study, and the present findings may serve as a starting point for future research.

Acknowledgements

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CHAPTER 2: BEHAVIORAL RESPONSE TO MULTI-CHANNEL ENVIRONMENTAL NOISE: TRACKING NOISE-INDUCED CHANGES IN MATE ATTRACTION STRATEGIES IN *ACHETA DOMESTICUS*

Introduction

Anthropogenic noise, carried in air, water, or through the substrate, is a well-recognized problem facing animals and can interact across multiple sensory modalities (Barber *et al.* 2010, Kight and Swaddle 2011, Luo *et al.* 2015). There are many physiological effects of noise, including changes in metabolism (Kight and Swaddle 2011), hearing impairment (Marler *et al.* 1973, Barber *et al.* 2010, Rabin *et al.* 2003), and an increase in hormone production (Francis and Barber 2013, Barber *et al.* 2010, Anderson *et al.* 2011, Chloupek *et al.* 2009, Gue *et al.* 1987). Behavior is also affected by noise. Noise can be a distraction, an irritant, or be perceived as a danger (Luo *et al.* 2015, Rabin *et al.* 2003, Francis and Barber 2013). There are many examples of lower population levels near sources of anthropogenic noise, as animals may try to avoid this irritant or perceived danger (Barber *et al.* 2010, Proppe *et al.* 2013). Perhaps the behavior most influenced by noise is communication.

In species using auditory communication, senders produce acoustic signals and receivers listen to and respond to these signals. Organisms which use acoustic communication for courtship and mating are particularly sensitive to anthropogenic noise, as noise may attenuate or alter the signal. Changes in courtship behavior may produce the greatest costs to an animal's reproductive fitness, as opportunities to mate may be missed, unless animals find a way to adjust courtship signals. This is quite widespread in birds (Patricelli and Blickley 2006). European robins, *Erithacus rubecula*, sing at night in areas that are noisy during the day, and show a diel pattern of communication to take advantage of temporal fluctuations in anthropogenic noise

(Fuller *et al* 2007). Some bird species adjust to urbanization, exhibiting adaptations to noise-related stressful conditions (Chace and Walsh 2006). Adaptations may involve changes in the timing of their calls. House sparrows, *Passer domesticus*, and spotless starlings, *Sturnus unicolor*, call earlier in the morning to avoid the morning rush of human noise (Arroyo-Solis *et al.* 2013). Another study on wild house sparrows, *Passer domesticus*, found increased vigilance behavior was used to compensate for a reduced ability to detect predators when noise was present (Meillère *et al.* 2015). Often, animals rely on communication (acoustic or otherwise) to mate, and any interruption in signal reception may result in missed mating opportunities, which, if severe and persistent, could lead to population decline. Noise also alters the way that predator cues are perceived, which may put animals in danger (Hartbauer *et al.* 2010; Morris-Drake *et al.* 2016).

Studies on the effects of noise on invertebrates, particularly insects, are comparatively limited. From an ecological perspective related to their important role across trophic levels, understanding how noise influences insect behavior and fitness represents a critical need. The ability to detect sound has evolved multiple times in insects, resulting in an array of auditory structures that can be found in almost any segment of the body (Morley *et al.* 2014). Insects may be the first animals to use airborne sound for long distance communication (Senter 2009) and do so mainly to attract mates (Gerhardt and Huber 2002). Crickets are a widely studied insect group that produce acoustic signals for pair formation and mating. Male crickets produce two calls: one for long distance mate attraction, and another, close range call for courtship after physical contact has occurred (Harrison *et al.* 2013, Rebar *et al.* 2009). Accurate reception of these signals is especially important for copulation as females will only mount males after they have called (Nelson and Nolen 1997, Stoffer and Walker 2012). House crickets, *Acheta domesticus*,

have been extensively studied in the field of communication and sensory biology. Although the importance of song in female choice has been studied in *A. domesticus* (Rek 2012, Stoffer and Walker 2012, Crankshaw 1979, Walikonis *et al.* 1991, Gray 1997, Gray 1999, Nelson and Nolan 1997, Stout and McGhee 1988), the effects of noise on male calling patterns in house crickets has not been studied

Due to the documented masking and distraction effects of noise (Francis and Barber 2013) on acoustically signaling species, *A. domesticus* males may adjust calling effort or avoid calling altogether when noise is present; no study has definitively described this however. Given the importance of the male call in facilitating mating for *A. domesticus*, the accurate transmission of the advertisement signal to the receiver target is directly linked to fitness outcomes. Females of a field cricket species, *Gryllus bimaculatus*, exhibited reduced phonotaxis when male calls were presented with noise, impeding mate localization and reproduction (Schmidt *et al.* 2014). Understanding how males respond to noise while calling may be key to unraveling how they, and other animal species, respond behaviorally to novel anthropogenic noise sources that cross sensory system boundaries.

The current study aims to answer the following question: How does noise across different sensory channels affect the daily calling patterns of male house crickets, *Acheta domesticus*? The following hypothesis were made: 1: Exposure to continuous noise will alter the overall calling activity in adult house crickets, with variable effects on the temporal patterns of calling. Due to signal masking, exposure to continuous isomodal noise (airborne) will result in an overall increase in calling activity in *A. domesticus* compared to control trials, with no change in the diel temporal pattern of calling over the 24-hour period. Sensory interference with the subgenual organ, which is involved with terrestrial predator detection and the resulting flight response, will

cause exposure to continuous crossmodal noise (substrate-borne vibration) to result in an overall decrease in daily calling activity in *A. domesticus* compared to control trials, with no change in the temporal pattern of calling over the 24-hour period. Due to sensory interference with both the subgenual and auditory organs, which are involved in both conspecific signal and predator detection, exposure to continuous multimodal noise (airborne plus substrate-borne vibration) will result in an overall decrease in daily calling activity in *A. domesticus* compared to control trials, with disruption of the diel temporal pattern of calling over the 24-hour period. 2: Exposure to noise during the peak male calling activity period only (intermittent noise) will alter the diel temporal pattern of calling but not influence the overall amount of calling in adult house cricket males. Due to signal masking, exposure to intermittent isomodal noise (airborne) during periods of peak calling activity will result in lowered calling activity in these peak periods and increased calling activity during typically quiescent periods. The overall amount of male calling will remain unchanged. Due to sensory interference with the subgenual organ, which is involved with terrestrial predator detection and the resulting flight response, exposure to intermittent crossmodal noise (substrate-borne vibration) during periods of peak calling activity will result in lowered calling activity in these peak periods and increased calling activity during typically quiescent periods. The overall amount of male calling will remain unchanged, but the effect will be greater than that of isomodal noise alone. Due to sensory interference with both the subgenual and auditory organs, which are involved in both conspecific signal and predator detection, exposure to intermittent multimodal noise (airborne plus substrate-borne vibration) during periods of peak calling activity will result in lowered calling activity in these peak periods and increased calling activity during typically quiescent periods. The overall amount of male calling

will remain unchanged, and while the effect will be greater than that of isomodal noise it will be no different than crossmodal noise.

Methods

Animals

Adult *A. domesticus* male crickets were obtained from a reseller (Petco®, Salem, New Hampshire) and were housed in the Integrative Animal Behavior Lab at the University of New Hampshire, Durham. Crickets were provided food and water *ad libitum*. Crickets were fed Meow Mix® original choice cat food, ground into a powder (30% crude protein, 11% crude fat, 4% crude fiber, 12% moisture); water was provided via soaked cotton balls placed in glass petri dishes. *A. domesticus* males were housed in 37.85 liter glass aquaria with mesh screen tops with recycled corrugated paper as refugia. Tanks were maintained at 23° Celsius and 46% relative humidity, in a 14:10 light/dark cycle. All noise trials were conducted in a hemi-anechoic chamber maintained in the same light, humidity and temperature regime.

Controls

An initial trial was conducted to determine the daily calling patterns in *A. domesticus* males maintained in laboratory conditions. 14 males were placed in a locomotor activity monitor (LAM; TriKinetics Inc. Waltham, MA), which allowed for the physical isolation of male subjects while monitoring acoustic activity (Figure 11). Food and water were placed at opposite ends of transparent Lexan tubes (2.5 cm wide x 8.0 cm long). One end of each tube was covered a plastic cap, and the other with acoustically transparent aluminum mesh screening to facilitate exposure to airborne noise during relevant treatments. The first 24 hours of each trial served as an acclimation period to account for enclosure effects. To describe diel patterns of male calling activity in *A. domesticus*, an omnidirectional microphone (identify mic details from FL

documentation if possible) connected to a Frontier Labs Bioacoustic Recorder was inserted into a hole drilled into the plastic cap end of the Lexan containment tube, such that the microphone fit snugly into the opening. The recorder was programmed to collect one-minute recordings (16 bit, 44.1 KHz WAV files) every 10 minutes during each 24-hour period for four days. I used the spectral view in Adobe Audition version 3.0 to identify male calling activity (Y/N) for each of the one-minute recordings (144 per 24-hour period). Calling data for each male was aggregated into two-hour bins, and identified by experimental test day (1-4). JMP Pro version 13 was used to conduct a Kruskal-Wallis test to identify differences between time blocks. Where time blocks differed, I conducted a post hoc test for differences between blocks using the Dunn's method for joint rankings. Time blocks were identified as follows: time block 1= 06:00-08:00, time block 2= 08:00-10:00, time block 3= 10:00-12:00, time block 4= 12:00-14:00, time block 5= 14:00-16:00, time block 6= 16:00-18:00, time block 7= 18:00-20:00, time block 8= 20:00-22:00, time block 9= 22:00-24:00, time block 10= 24:00-02:00, time block 11= 02:00-04:00, and time block 12= 04:00-06:00. The peak calling period identified during control tests served as the presentation period for all intermittent noise playbacks (isomodal airborne noise, crossmodal substrate borne vibration, and a combination of both for a multimodal noise stimulus).

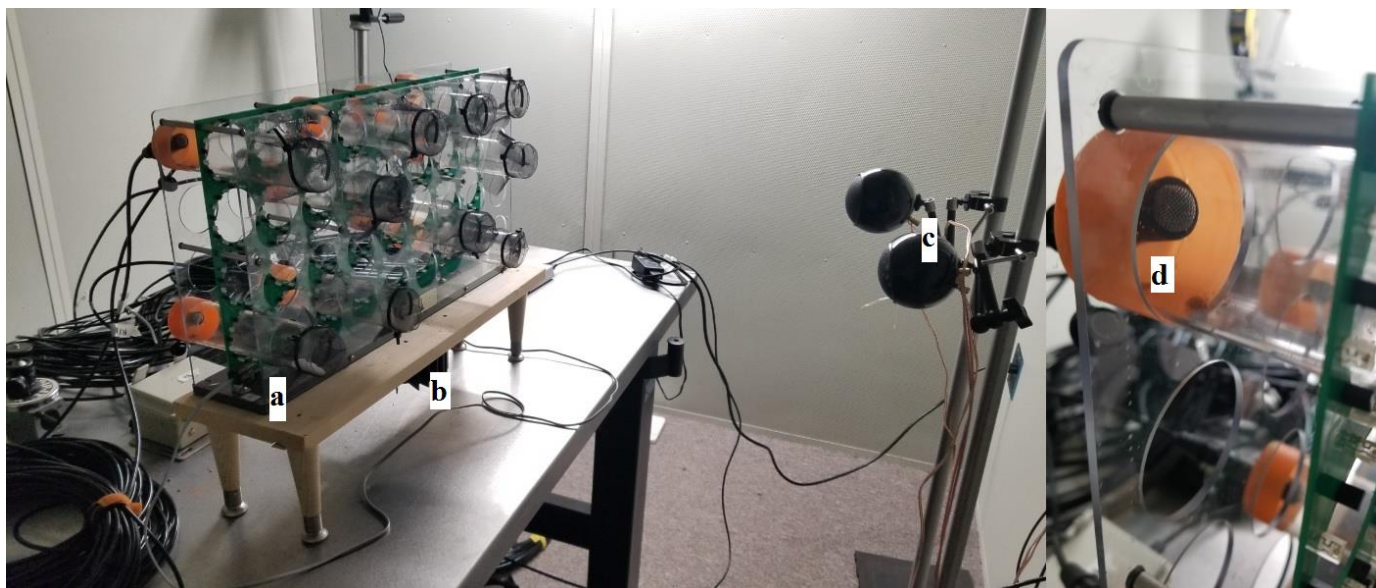


Figure 11: The experimental setup. The monitor (a) is placed on a wooden platform where an electromagnetic bass shaker plays substrate-borne vibrational noise (b). Two speakers (c) play airborne white noise. Each tube contains a microphone connected to a programmable acoustic recorder (d) to record male calling activity.

Isomodal Noise Exposure

The airborne noise stimulus used for isomodal noise playbacks and included in the multimodal noise playback series was created in Adobe Audition version 3.0 and consisted of a 60-second series of 500-ms pulses of white noise (20-22050 Hz) interspersed by 5-sec inter-pulse intervals. The 60-second sound file was played back on a loop through two speakers (Orb Audio Mod1) positioned 1 m from the face of the LAM prep and calibrated to 85 dB SPL using a Brüel and Kjær 2250 Lite sound pressure meter. Each isomodal noise treatment lasted five days, with the first day being used as an acclimation period to account for enclosure effects. For intermittent noise trials, the stimulus was presented during the peak calling activity period identified during controls, and played back over the course of four experimental days during these peak calling periods. For continuous noise trials, the noise stimulus was played continuously for the entire four-day experimental period. Male calling was recorded as detailed previously in controls, and data aggregated into the same two-hour bins. Binned male calling data were then analyzed in JMP Pro version 13 using a Kruskal-Wallis test to identify

differences between time blocks. Where time blocks differed, I conducted a post hoc test for differences between blocks using the Dunn's method for joint rankings.

Crossmodal Noise Exposure

The substrate-borne vibration stimulus used for crossmodal and multimodal noise treatments was a 60-second train of 500-ms vibration pulses (brown noise, generated and band pass filtered in Adobe Audition version 3.0 to generate most energy between 10-300 Hz) with 5-sec inter-pulse intervals that was used in looped playbacks during the specified presentation period. In treatments with substrate-borne noise (crossmodal and multimodal conditions), an electromagnetic shaker (AuraSound, Inc. AST-2B-04 50-Watt bass shaker) was bolted to the underside of a custom raised platform (61x18x13 cm) on the top of which was affixed the locomotor activity monitor used to isolate males in all trials. The shaker was powered by an ART SLA4 4-Channel 140 Watt amplifier (ART ProAudio, Niagara Falls, NY) and was calibrated before each trial with a Polytech PDV-100 laser Doppler vibrometer (Polytec GmbH, Waldbronn, Germany) to an amplitude of 15.0 mm/sec (9.4 m/s²). As in all other trials, each treatment lasted five days, with the first day being used as an acclimation period. For intermittent noise trials, the stimulus was presented during the previously determined peak male calling period over the course of the four noise exposure days. For continuous noise trials, the stimulus was played for the entire four-day experimental period. Male calling was recorded as detailed previously in controls, and data aggregated into the same two-hour bins. Binned male calling data were then analyzed in JMP Pro version 13 using a Kruskal-Wallis test to identify differences between time blocks. Where time blocks differed, I conducted a post hoc test for differences between blocks using the Dunn's method for joint rankings.

Multimodal Noise Exposure

Multimodal noise treatments consisted of both airborne and substrate-borne stimuli parameterized and calibrated as in the isomodal and crossmodal trials, presented synchronously. Each multimodal treatment lasted five days, with the first day being used as an acclimation period. For intermittent multimodal noise trials, the combined airborne and substrate-borne noise stimulus was presented during the previously determined peak locomotor activity period over the course of the four noise exposure days. For continuous noise trials, the multimodal stimulus was played for the entire four-day period. Male calling was recorded as detailed previously in controls, and data aggregated into the same two-hour bins. Binned male calling data were then analyzed in JMP Pro version 13 using a Kruskal-Wallis test to identify differences between time blocks. Where time blocks differed, I conducted a post hoc test for differences between blocks using the Dunn's method for joint rankings.

Results

Control

For control conditions (n=14 males), a Kruskal-Wallis one-way test indicated that the number of calls per time block were significantly different (χ^2 approximation $X^2 = <0.0001$, $df = 11$, $P < 0.0001$, Dunn Method for Joint Rankings $P < 0.0001$). *Acheta domesticus* males exhibited peak calling activity during time blocks 11 (02:00-04:00) and 12 (04:00-06:00) (Figure 11), with male calling detected in 9 mins and 8 mins out of 12 possible, respectively. Time blocks 11 and 12 were not significantly different from each other (Dunn method $P = 1.000$), thus these two time blocks served as the presentation period for subsequent intermittent noise stimulus trials (isomodal, crossmodal, and multimodal).

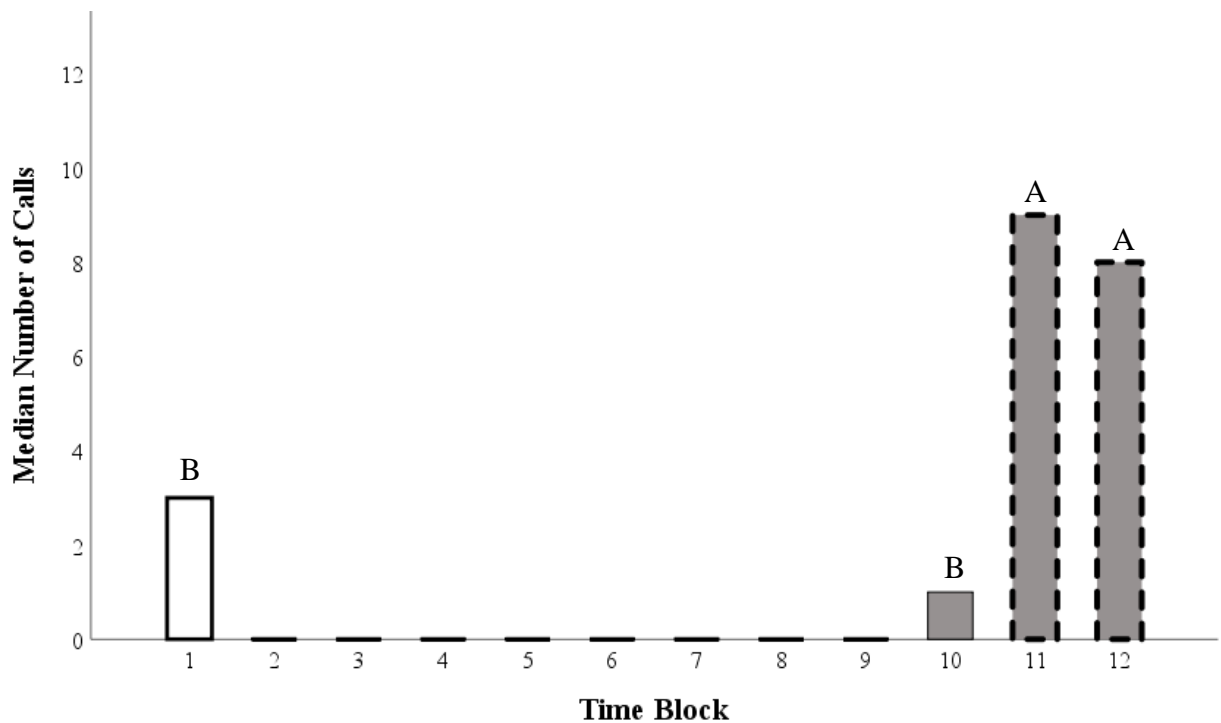


Figure 12: Median number of calls per two-hour time block in controls. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). During each time block, 12 recordings were taken, resulting in 12 possible call detections. The highest number of calls were observed during time blocks 11 and 12 (indicated with dashed lines), or from 02:00-06:00.

Isomodal Noise

Intermittent isomodal noise playback trials (airborne sound; n=19) were conducted between 02:00 am and 06:00 am for four days. The number of call detections per time block was significantly different across the time blocks (Kruskal-Wallis test, one-way Chi-square approximation $X^2 = <0.0001$, d.f. = 11, $P < 0.0001$). The peak calling period in this experimental trial was observed in time blocks 8 through 12 (20:00-08:00; Figure 12), with calling activity recorded in all 12 observation periods. The first two hours of light (time block 1, 06:00-08:00) also saw an increase in calling activity as compared to controls, with calling activity recorded in nine out of 12 possible observation periods. Lower levels of calling activity was also detected during light time blocks 2-7. Differences in calling activity between time blocks 1 and 8-12 and time blocks 2-7 were all significant (post hoc Dunn's test, $P < 0.0001$, Figure 13).

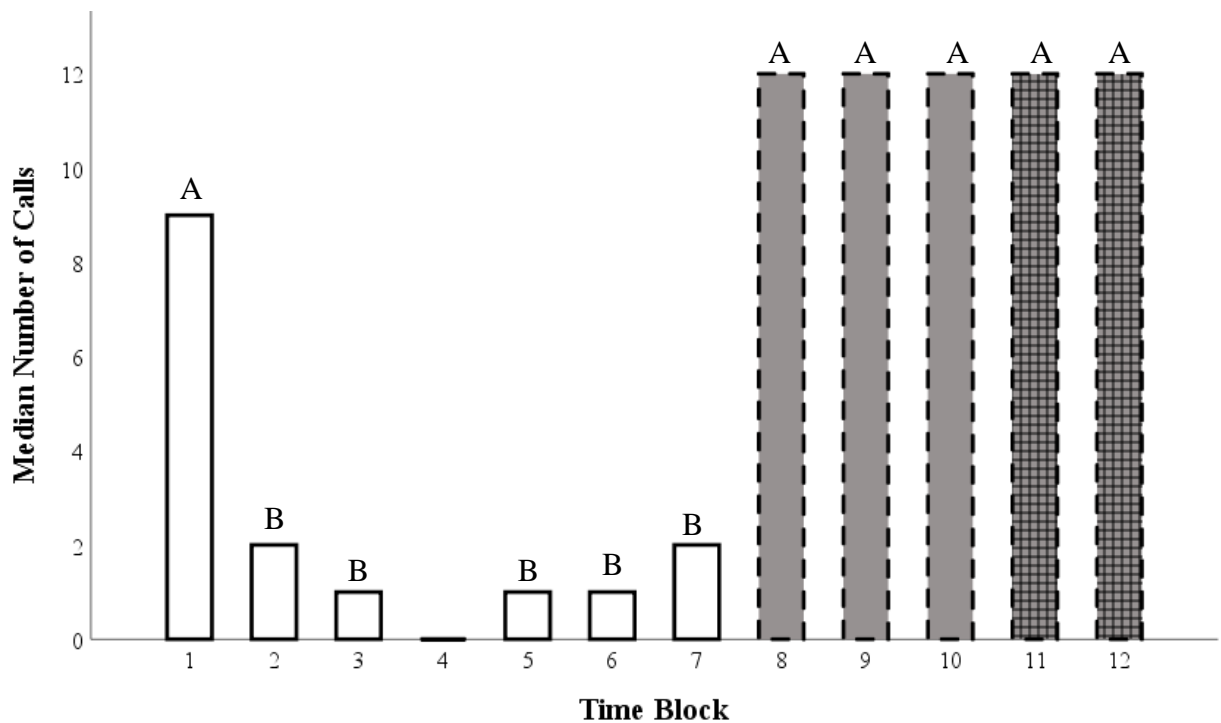


Figure 13: Median number of calls per two-hour time block, intermittent isomodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). During each time block, 12 recordings were taken, resulting in 12 possible call detections. Intermittent isomodal noise was played during the peak calling period found in control conditions (Time blocks 11 and 12, or 02:00-06:00, indicated with grid pattern). Peak calling period extended from 02:00-06:00 to 20:00-06:00 (Time blocks 8 through 12, indicated with dashed lines).

Continuous isomodal noise exposure ($n = 20$) resulted in a similar change in calling pattern to that seen with intermittent isomodal noise. The number of call detections per time block was significantly different across the time blocks (Kruskal-Wallis test, one-way Chi-square approximation $X^2 = <0.0001$, d.f. = 11, $P < 0.0001$). Male calling activity peaked in time blocks 9 through 12 (22:00-08:00; Figure 14), with calling activity recorded in all 12 observation periods. The peak calling period extended from 02:00-06:00 to 22:00-06:00 (see Figure 14), with 11 detections in time block 9, and 12 out of 12 possible detections in time blocks 10 through 12. The first two hours of light (time block 1, 06:00-08:00) also saw an increase in calls compared to control, with six out of 12 possible detections. Lower levels of calling activity was also detected

during light time blocks 2 and 8. Differences between time blocks 9-12 and time blocks 1-7 were all significant (post hoc Dunn's test, $P < 0.0001$).

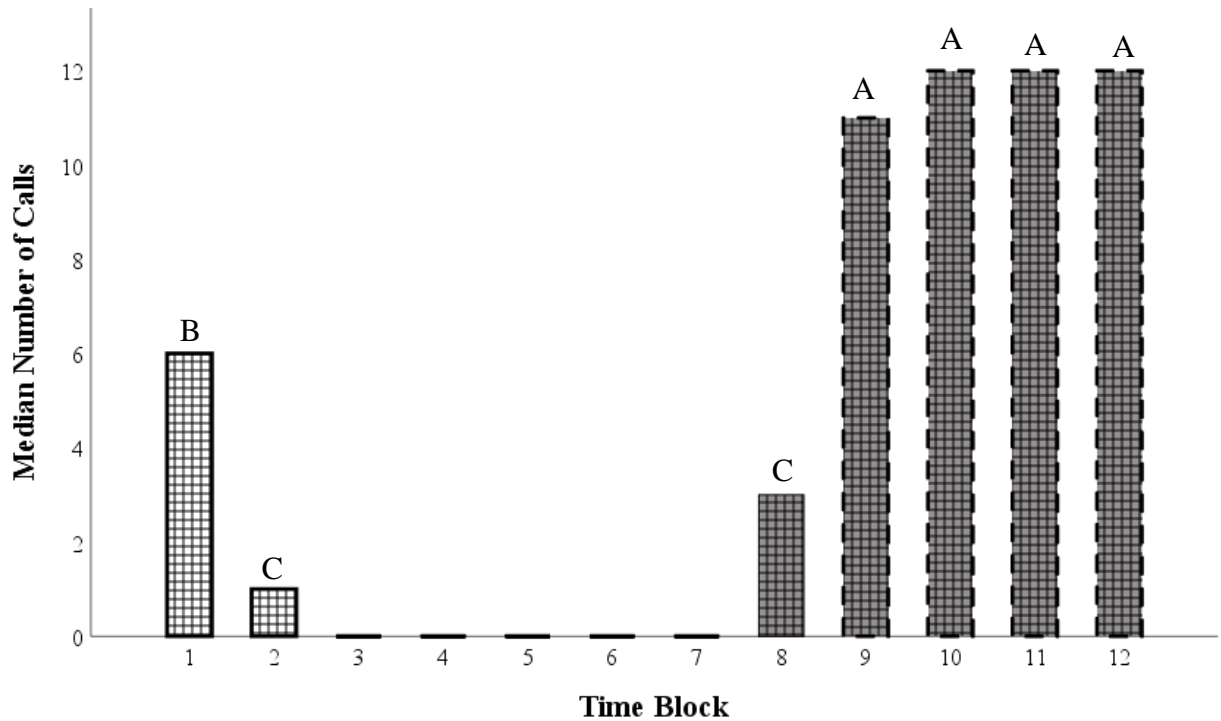


Figure 14: Median number of calls per time block, continuous isomodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). During each time block, 12 recordings were taken, resulting in 12 possible call detections. Peak calling periods were observed in time blocks 9-12 (22:00-06:00), indicated with dashed lines.

Crossmodal Noise

Intermittent crossmodal noise playback trials (substrate-borne vibration; $n=20$) were conducted between 02:00 and 06:00 for four days. The number of call detections per time block was significantly different across the time blocks (Kruskal-Wallis test, one-way Chi-square approximation $X^2 = < 0.0001$, d.f. = 11, $P < 0.0001$). The peak calling period in this experimental trial was observed in time blocks 8-12 (20:00-06:00; Figure 15), with calling activity observed in eight to 12 observation periods during these time blocks. Lower levels of calling activity was

also detected during light time blocks 1-3. Differences between time blocks 1 and 8-12 and time blocks 2-7 were all significant (post hoc Dunn's test, $P < 0.0001$).

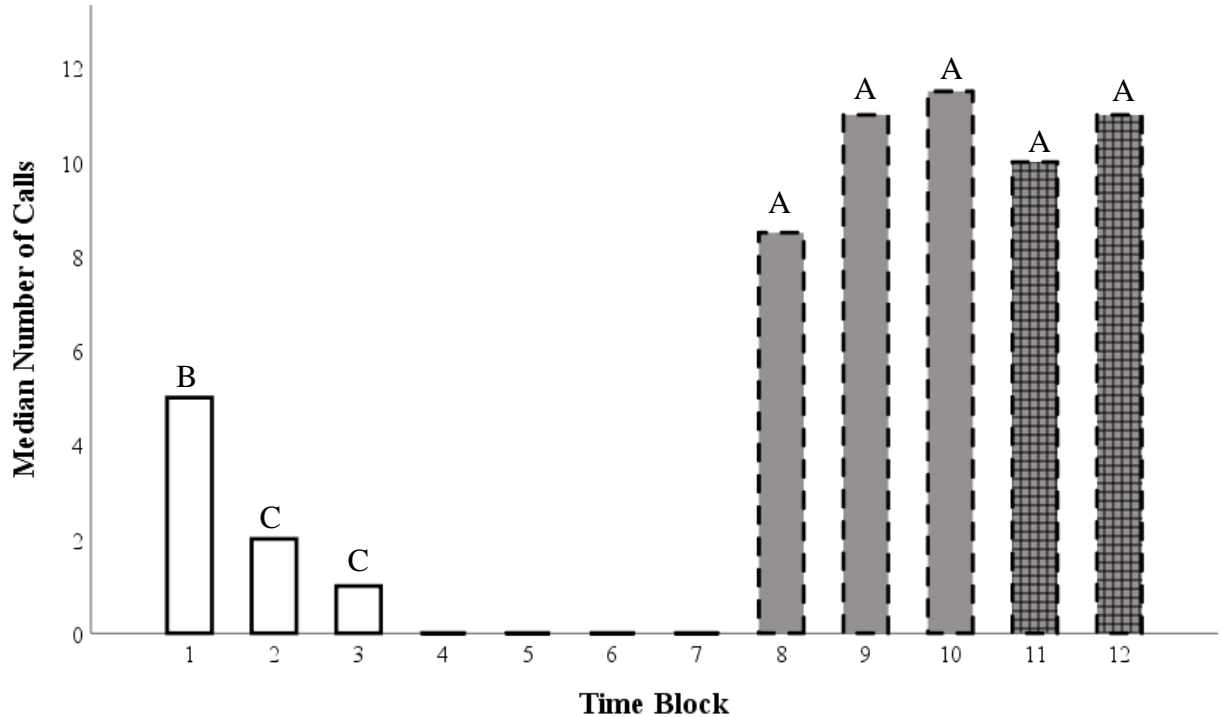


Figure 15: Median number of calls per two-hour time block, intermittent crossmodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). During each time block, 12 recordings were taken, resulting in 12 possible call detections. Intermittent crossmodal noise was played from 0:00-06:00 (indicated with grid pattern). Peak calling increased from 02:00-06:00 to 20:00-06:00 (indicated with dashe lines), and calling during the day increased.

Continuous crossmodal noise exposure ($n = 20$) resulted in a similar change in calling pattern to that seen with intermittent crossmodal noise. The number of call detections per time block was significantly different across the time blocks (Kruskal-Wallis test, one-way Chi-square approximation $X^2 = <0.0001$, d.f. = 11, $P < 0.0001$). The peak calling period in this experimental trial was observed in time blocks 9-12 (22:00-08:00; Figure 16), with 12 out of 12 possible detections in time block 12, 11 in time block 11, 10 in time block 10, and nine in time block 9. Lower levels of calling activity was also detected during light time blocks 1, 2, 3 and 8.

Differences between time blocks 1, and 9-12 and time blocks 2-8 were all significant (post hoc Dunn's test, $P < 0.0001$).

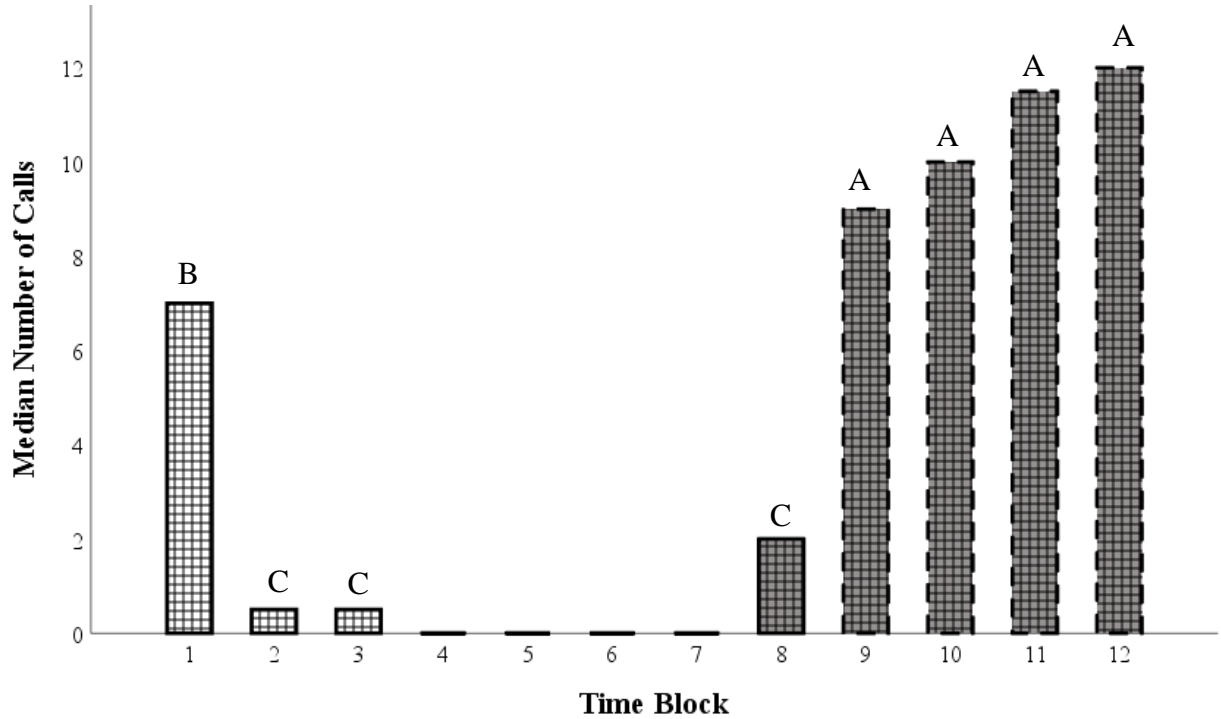


Figure 16: Median number of calls per time block, continuous crossmodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). During each time block, 12 recordings were taken, resulting in 12 possible call detections. Peak calling increased from 02:00-06:00 to 22:00-06:00 (indicated with dashed lines), and calling during the day increased.

Multimodal Noise

Intermittent multimodal noise playback trials (airborne sound combined with substrate-borne vibration combined; $n=20$) were conducted between 02:00 and 06:00 for four days. The number of call detections per time block was significantly different across the time blocks (Kruskal-Wallis test, one-way Chi-square approximation $X^2 = < 0.0001$, d.f. = 11, $P < 0.0001$). The peak calling activity in this experimental trial was observed split between time blocks 9-10 (22:00-02:00) and time block 12 (04:00-06:00; Figure 17), with calling activity recorded in 12 out of 12 possible observation periods in these blocks. Secondary calling peaks were observed in time blocks 1, 8 and 11, with lower levels of calling activity detected during light time blocks 2-

7. Differences between time blocks 1 and 8-12 and time blocks 2-7 were all significant (post hoc Dunn's test, $P < 0.0001$).

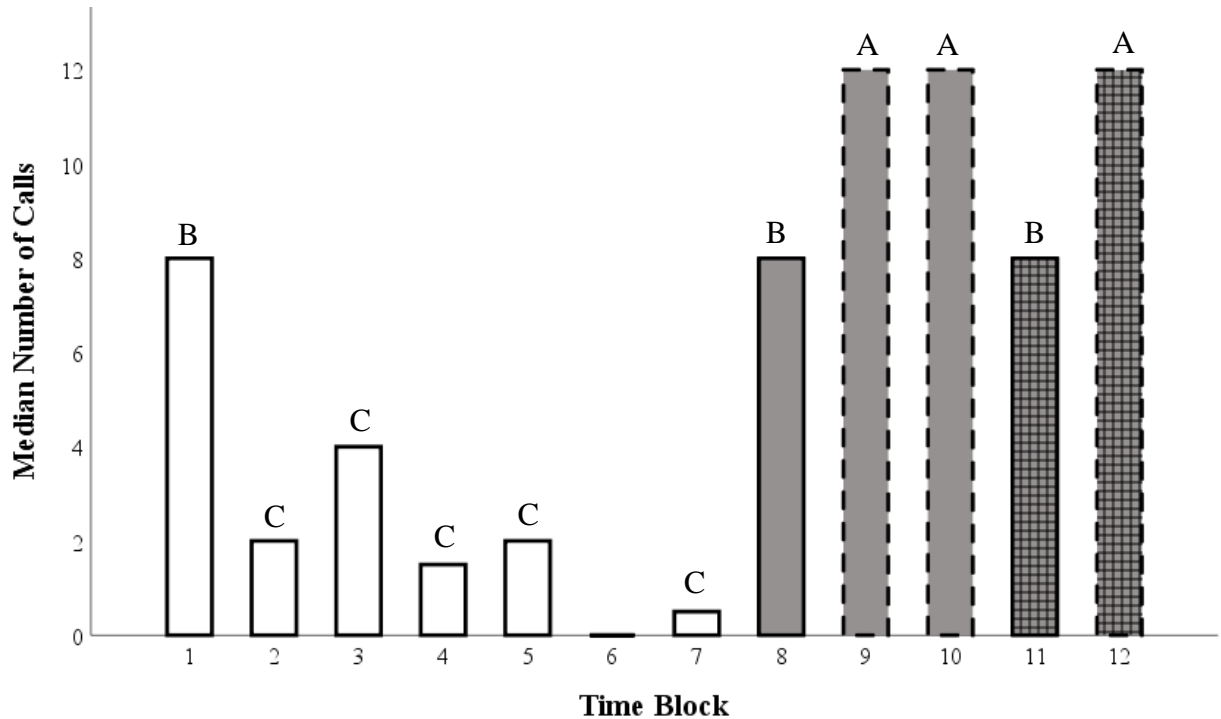


Figure 17: Median number of calls per two-hour time block, intermittent multimodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). Intermittent crossmodal noise was played from 0:00-06:00 (indicated with grid pattern). During each time block, 12 recordings were taken, resulting in 12 possible call detections. The peak calling period shifted from 02:00-06:00 to a split between times block 9-10 (22:00-02:00) and time block 12 (04:00-06:00), indicated with dashed lines.

Continuous multimodal noise exposure ($n = 20$) resulted in a decrease in calling activity, and a change in the daily pattern compared to control conditions. The number of call detections per time block in this treatment condition was significantly different across the time blocks (Kruskal-Wallis test, one-way Chi-square approximation $X^2 = < 0.0001$, d.f. = 11, $P < 0.0001$). The peak calling period occurred during time blocks 11 and 12 as in control conditions, however, the number of recordings during observation periods declined to 7 out of 12 (Figure 18). Observed calling activity was reduced over all other time blocks when compared to other

playback treatments. Significant differences in calling activity were observed between time blocks 1, and 9-12 and time blocks 2-8 (post hoc Dunn's test, $P < 0.0001$).

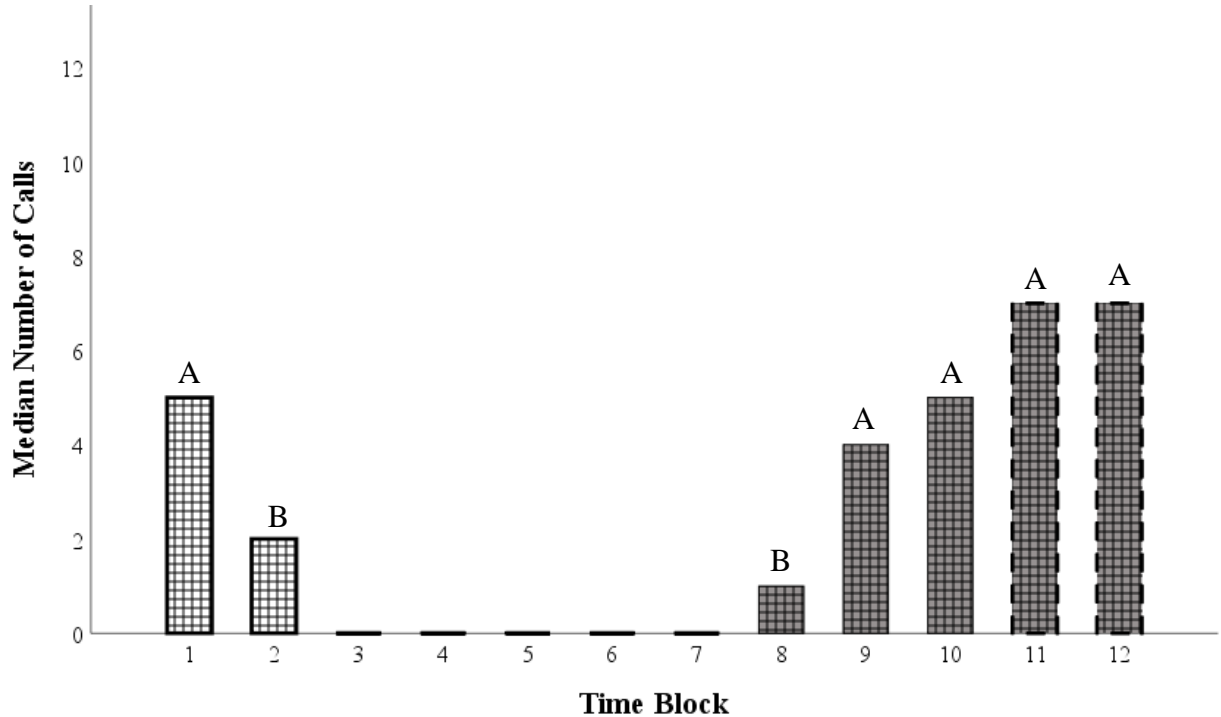


Figure 18: Median number of calls per time block, continuous multimodal noise. White bars indicate when the lights were on (06:00-20:00), and gray bars indicate when the lights were off (20:00-06:00). During each time block, 12 recordings were taken, resulting in 12 possible call detections. The peak calling period includes time blocks 11 and 12 (02:00-06:00, indicated with dashed lines), just as in control conditions. However, only seven out of 12 recordings contained calls. Calling activity was dramatically reduced overall with continuous multimodal noise playback.

Overall male calling activity differed between treatments (Figure 19; Kruskal-Wallis test, one-way Chi-square approximation $X^2 = < 0.0001$, d.f. = 6, $P < 0.0001$). All treatments differed in overall total male calling activity, with the exception of continuous multimodal noise (post hoc Dunn's test, $p = 0.0746$ for continuous multimodal noise, $P < 0.0001$ for all other comparisons to control).

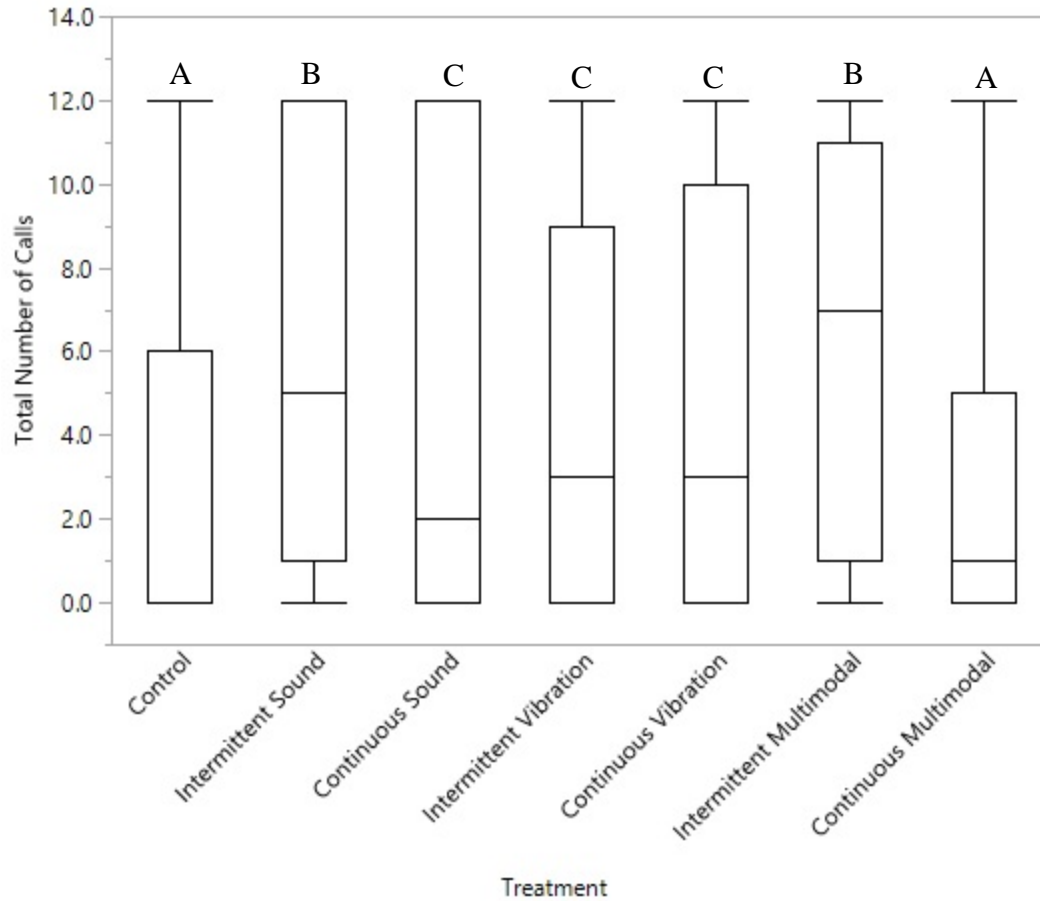


Figure 19: Number of calls (median and IQ ranges) for control and noise treatments. Intermittent multimodal noise exposure produced the largest net effect, significantly increasing the overall amount of male calling, while also disrupting diel patterns. Continuous multimodal noise suppressed calling activity without altering diel patterns. In all other treatment conditions, males increased the amount of time spent calling compared to control conditions.

Discussion

Laboratory cultures of *Acheta domesticus* exhibited nocturnal calling patterns, with the most calling occurring between 02:00 and 06:00. This is consistent with previous studies on the species (Nowosielski and Patton 1963, Sokolove 1975). When exposed to noise during peak calling periods, response differed depending on the noise modality of the stimulus. With intermittent isomodal noise (airborne sound), *A. domesticus* males called for a longer period of time, beginning when the lights went off at 20:00, and calling almost continuously until the lights came back on at 06:00 (12 out of 12 recordings for each time block contained calls). In

addition, more calls were recorded during the first two hours of light during time block 1 (06:00-08:00). It appears that males are adjusting to the temporary disruption in the soundscape by increasing the amount of time spent calling, ostensibly to increase the chances of attracting a mate. In crickets, males sing to attract females, and it is the female that mounts the male for copulation; if a female has not heard a male call, she will not mate with him (Nelson and Nolen 1997). However, increasing the time spent advertising likely increases the chance that an eavesdropper (a potential predator/parasitoid) may detect a male, and thus increase in calling effort likely poses a predation cost, in addition to the net increase in metabolic investments related to calling.

Similar results were observed with exposure to continuous isomodal noise, along with intermittent and continuous crossmodal noise, and intermittent multimodal noise. Continuous multimodal noise exposure resulted in a similar diel pattern of calling as compared to controls, however the amount of time invested in calling decline. It is possible that this is due to a form of “sensory overload” caused by the constant noise interfacing with multiple sensory modalities, introducing both perceived signal masking effects and predation cues. Or this complex form of noise may act as an irritant or distraction. Laboratory rodents become irritable when exposed to chronic noise and can even become aggressive and reduce food intake (Anthony and Ackerman 1955, Sackler *et al.* 1959). In Daubenton’s bats, *Myotis daubentonii*, traffic noise acts as an aversive stimulus and decreases foraging effort and efficiency. Noise does not actually block the bats’ echolocation, rather it distracts them from accurately using there echolocation properly (Luo *et al.* 2015). Terrestrial hermit crabs, *Coenobita clypeatus*), hid from perceived danger (in the form of a visual stimulus) more slowly when white noise was present (Chan *et al.* 2010). The question remains however, why was this suppressive effect only observed during continuous

multimodal noise exposure. Other stimulus trials resulted in an increase in calling outside of peak hours, both in continuous and intermittent trials. It appears that *A. domesticus* responds very differently to different forms and durations of noise exposure. Males made the decision to call more in all trials except continuous multimodal noise, in which case they reduced calling effort but maintained typical diel calling activity patterns. This response was not seen with intermittent multimodal noise exposure, so being exposed for four hours apparently was still “tolerable” to male *A. domesticus*, while continuous multimodal exposure becomes too much of either a distraction or an irritant to keep calling. Perhaps males are aware that the investment in producing calls is no longer worth the payback, as either females will not be able to hear them, or the risk of predation is too high (or potentially both).

The findings of this study have enormous implications for insect mating systems which rely on acoustic communication. In particular, this study demonstrates that insects, in this case crickets, have the capacity to adjust their calling patterns and duration in response to different forms of noise. These adjustments have implications for fitness, with increased calling effort likely to cost more energetically but potentially increase their likelihood of securing a mate. However, it appears that exposure to continuous multimodal noise impedes the organism’s ability to adjust calling behavior and likely imposes direct detrimental effects on their reproductive fitness. In addition to reproductive costs, animals, insects in particular, may face different predation risks by calling during a different part of the day. If a calling cricket has changed its calling patterns to call during the day, there may be new predators that can eavesdrop, that were avoided during nocturnal calling. All noise treatments except for multimodal continuous noise resulted in males adjusting their natural daily calling patterns to call outside of the periods of noise exposure. This behavior plasticity in response to ambient

noise challenges may result in exposure to a new community of acoustically eavesdropping predators, and might decouple advertisement timing from peak female mate searching time windows.

It is also important to note that in the present experiment, male *A. domesticus* movements were limited to the confines of the plastic tubes of the locomotor activity monitor. Perhaps given the opportunity, males would flee the source of noise and relocate to call elsewhere. However, my findings highlight the importance of the acoustic structure and exposure duration of noise in driving behavioral response in animals broadly, with specific implications for beneficial insect populations, a group often ignored in discussions of noise effects on ecosystems. In particular, insect populations exposed to persistent noise may experience population declines, altering community structures. Given that anthropogenic noise will likely only increase in prevalence and complexity in the future, further research is needed to understand species-specific impacts leading to community and ecosystem-level disruptions.

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CONCLUSION

With the current experiments, I have found that *Acheta domesticus* alters its behavior in response to noise. Behavioral changes were seen in response to intermittent and continuous isomodal, crossmodal, and multimodal noise. Two behaviors were measured in these experiments (locomotion and calling patterns), and both were altered in response to noise. The first step in both experiments was to establish a circadian rhythm/natural diel activity pattern for these two behaviors. Most adult locomotory behavior occurred between 12:00 and 16:00, and most male calling occurred between 02:00 and 06:00. The behaviors do not show much overlap, which is consistent with a previous study on *Teleogryllus commodus*, with locomotion occurring mostly during the day, and calling at night (Sokolove 1975). The cricket mating process usually consists of males remaining stationary and calling to females, who approach, engage the male in courtship behaviors, and choose whether or not to mount the male for copulation (Stoffer and Walker 2012, Nelson and Nolan 1997). As was found in chapter 2, males call during the dark hours (02:00-06:00), so it would make sense that they would not be moving much during this time, but rather they are waiting for females to locate them.

When considering locomotion alone, there is some inconsistency among previous studies as to what the daily activity pattern looks like for *A. domesticus*. Lutz (1932) found high activity during the first half of the night. A later study by Nowosielski and Patton (1963) found high individual variation in activity with often more than a single peak. The study looked at adults and last larval instars and found that last larval instar crickets were less active than adults and had almost no pattern in activity. With adults, some individuals had one peak of activity right after the onset of dark, and others exhibited a second peak of activity before dark. The authors note

that not all crickets in the study fell into one category or the other, but that the pattern remained consistent after crickets had their last molt. An important reason for this individual variation is thought to be related to allowing for greater utilization of the environment in time. My experiment shows a peak locomotor period of 12:00-16:00, which falls within the second peak observed by Nowosielski and Patton (which started between 14:00 and 15:30), though no evening peak was found. It should be noted that Nowosielski and Patton raised crickets under a different light cycle (12:12 08:00-20:00 versus 14:10 in my study).

Each form of noise produced a different response in locomotion. A suppressive response can be seen with continuous airborne and continuous multimodal noise. Because the normal daily pattern of locomotion has been interrupted, it is possible that fitness consequences could be seen. If *A. domesticus* is experiencing a startle response by remaining stationary more often with continuous noise, this could mean that less time is being spent on task crucial to survival, including foraging, finding shelter, or finding a mate. Noise changed the daily pattern of locomotion in all noise treatments, meaning that these consequences may be seen in conditions other than continuous iso- and multimodal noise. Remaining stationary could make *A. domesticus* an easy target for predators, which may alter population levels and food chains over the long term. This is an important factor to consider when applying these findings to other species. Perhaps some species will be better at dealing with anthropogenic noise than others, but there is no way to know this without further study, and the present findings may serve as a starting point for future research.

When exposed to noise during the peak calling period (02:00-06:00), male house crickets' response differed depending on the sensory modality used to perceive noise. It appears that males are adjusting to the temporary disruption in the soundscape by increasing the amount

of time spent calling, ostensibly to increase the chances of finding a mate. Continuous multimodal noise exposure resulted in a similar pattern of calling over the course of the day as other treatments, however the number of minutes per time block invested in calling declined dramatically. Continuous multimodal noise is the only treatment that did not differ from control in terms of magnitude of calls, however the shift in diel calling pattern was consistent with other noise treatments. It is possible to explain this as a form of “sensory overload” caused by the constant noise coming from multiple sensory modalities. Crickets may be perceiving this noise as an irritant or distraction, which has been observed in other taxa. Laboratory rodents become irritable when exposed to chronic noise and can even become aggressive and reduce food intake (Anthony and Ackerman 1955, Sackler *et al.* 1959). In Daubenton’s bats, *Myotis daubentonii*, traffic noise acts as an aversive stimulus and decreases foraging efficiency. Noise is not blocking the bats’ echolocation, rather it distracts them from using their echolocation properly (Luo *et al.* 2015). Terrestrial hermit crabs, *Coenobita clypeatus*, hid from perceived danger (in the form of a visual stimulus) more slowly when white noise was present (Chan *et al.* 2010). It would seem that the crabs were unable to focus on more than one type of sensory input at a time. The question remains however, why was this effect only seen in continuous multimodal noise with *A. domesticus*? Perhaps males are aware that the investment in producing calls is no longer worth the effort, as females will not be able to hear them. This has enormous implications to mating, and therefore reproductive fitness of this species. these results may apply to other cricket species, and possibly even other insects and other taxa. Anthropogenic noise will only increase in the coming years, and further research is needed to understand the impact it may have on animals.

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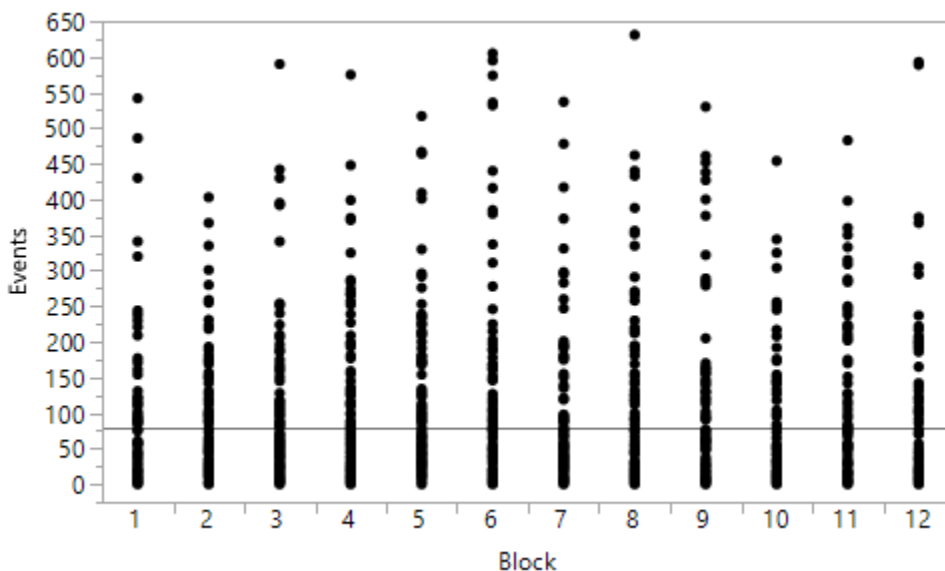
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APPENDIX A: JMP RESULTS FOR CHAPTER 1

Control

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	128	82494.0	98368.0	644.484	-3.312
2	128	105340	98368.0	822.965	1.455
3	128	102411	98368.0	800.086	0.844
4	128	111407	98368.0	870.363	2.721
5	128	118413	98368.0	925.102	4.183
6	128	110030	98368.0	859.605	2.433
7	128	108224	98368.0	845.500	2.057
8	128	106721	98368.0	833.758	1.743
9	128	86552.5	98368.0	676.191	-2.465
10	128	80308.0	98368.0	627.406	-3.768
11	128	85459.0	98368.0	667.648	-2.694
12	128	83058.0	98368.0	648.891	-3.195

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
82.1630	11	<.0001*

Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

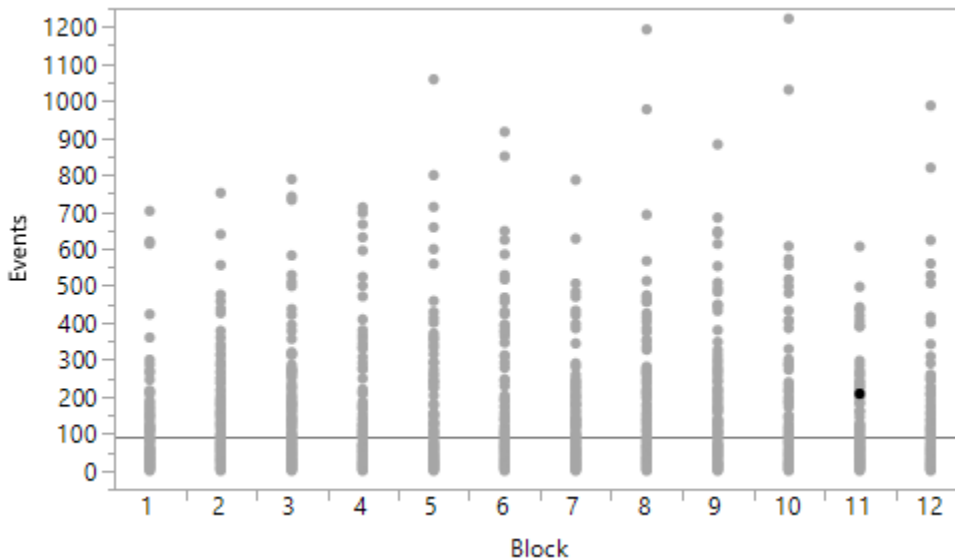
Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
5	1	280.609	55.30150	5.07417	<.0001*
4	1	225.871	55.30150	4.08436	0.0029*
6	1	215.113	55.30150	3.88983	0.0066*
7	1	201.008	55.30150	3.63476	0.0184*
8	1	189.266	55.30150	3.42243	0.0410*

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
2	1	178.473	55.30150	3.22727	0.0825
3	1	155.594	55.30150	2.81355	0.3234
5	3	125.008	55.30150	2.26048	1.0000
5	2	102.129	55.30150	1.84677	1.0000
4	3	70.270	55.30150	1.27066	1.0000
6	3	59.512	55.30150	1.07613	1.0000
5	4	54.730	55.30150	0.98967	1.0000
4	2	47.391	55.30150	0.85695	1.0000
7	3	45.406	55.30150	0.82107	1.0000
11	10	40.234	55.30150	0.72755	1.0000
6	2	36.633	55.30150	0.66242	1.0000
8	3	33.664	55.30150	0.60874	1.0000
9	1	31.699	55.30150	0.57321	1.0000
11	1	23.156	55.30150	0.41873	1.0000
7	2	22.527	55.30150	0.40735	1.0000
12	10	21.477	55.30150	0.38835	1.0000
8	2	10.785	55.30150	0.19502	1.0000
12	1	4.398	55.30150	0.07954	1.0000
11	9	-8.535	55.30150	-0.15434	1.0000
6	4	-10.750	55.30150	-0.19439	1.0000
8	7	-11.734	55.30150	-0.21219	1.0000
7	6	-14.098	55.30150	-0.25492	1.0000
10	1	-17.070	55.30150	-0.30868	1.0000
12	11	-18.750	55.30150	-0.33905	1.0000
3	2	-22.871	55.30150	-0.41357	1.0000
7	4	-24.855	55.30150	-0.44945	1.0000
8	6	-25.840	55.30150	-0.46725	1.0000
12	9	-27.293	55.30150	-0.49353	1.0000
8	4	-36.598	55.30150	-0.66178	1.0000
10	9	-48.777	55.30150	-0.88203	1.0000
6	5	-65.488	55.30150	-1.18420	1.0000
7	5	-79.594	55.30150	-1.43927	1.0000
8	5	-91.336	55.30150	-1.65160	1.0000
9	3	-123.887	55.30150	-2.24021	1.0000
11	3	-132.430	55.30150	-2.39469	1.0000
9	2	-146.766	55.30150	-2.65392	0.5251
12	3	-151.188	55.30150	-2.73388	0.4131
11	2	-155.309	55.30150	-2.80840	0.3286
9	8	-157.559	55.30150	-2.84908	0.2894
11	8	-166.102	55.30150	-3.00356	0.1761
9	7	-169.301	55.30150	-3.06141	0.1454
10	3	-172.672	55.30150	-3.12237	0.1184
12	2	-174.066	55.30150	-3.14759	0.1087
11	7	-177.844	55.30150	-3.21589	0.0858
9	6	-183.406	55.30150	-3.31648	0.0602
12	8	-184.859	55.30150	-3.34275	0.0547
11	6	-191.949	55.30150	-3.47096	0.0342*
9	4	-194.164	55.30150	-3.51101	0.0295*
10	2	-195.551	55.30150	-3.53608	0.0268*
12	7	-196.602	55.30150	-3.55509	0.0249*
11	4	-202.707	55.30150	-3.66549	0.0163*
10	8	-206.344	55.30150	-3.73125	0.0126*

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
12	6	-210.707	55.30150	-3.81015	0.0092*
10	7	-218.086	55.30150	-3.94358	0.0053*
12	4	-221.465	55.30150	-4.00468	0.0041*
10	6	-232.191	55.30150	-4.19865	0.0018*
10	4	-242.949	55.30150	-4.39318	0.0007*
9	5	-248.902	55.30150	-4.50082	0.0004*
11	5	-257.445	55.30150	-4.65530	0.0002*
12	5	-276.203	55.30150	-4.99450	<.0001*
10	5	-297.688	55.30150	-5.38299	<.0001*

Intermittent Isomodal Noise

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	204	205067	249798	1005.23	-4.638
2	204	308835	249798	1513.89	6.121
3	204	274118	249798	1343.72	2.522
4	204	250599	249798	1228.43	0.083
5	204	244838	249798	1200.19	-0.514
6	204	268356	249798	1315.47	1.924
7	204	259932	249798	1274.18	1.051
8	204	273148	249798	1338.96	2.421
9	204	234050	249798	1147.30	-1.633
10	204	225898	249798	1107.34	-2.478
11	204	224620	249798	1101.08	-2.611
12	204	228118	249798	1118.23	-2.248

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
88.8726	11	<.0001*

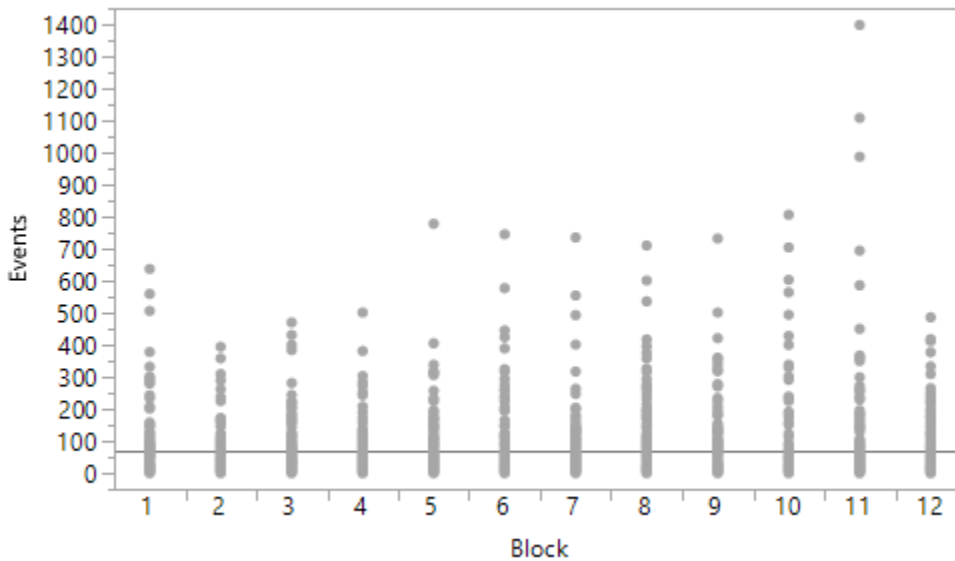
Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
2	1	508.662	69.83398	7.28387	<.0001*
3	1	338.483	69.83398	4.84696	<.0001*
8	1	333.728	69.83398	4.77888	0.0001*
6	1	310.235	69.83398	4.44247	0.0006*
7	1	268.944	69.83398	3.85119	0.0078*
4	1	223.194	69.83398	3.19606	0.0919
5	1	194.953	69.83398	2.79167	0.3461
9	1	142.069	69.83398	2.03438	1.0000
8	5	138.770	69.83398	1.98714	1.0000
6	5	115.277	69.83398	1.65073	1.0000
12	1	112.993	69.83398	1.61802	1.0000
8	4	110.529	69.83398	1.58275	1.0000
10	1	102.108	69.83398	1.46215	1.0000
11	1	95.843	69.83398	1.37244	1.0000
6	4	87.037	69.83398	1.24634	1.0000
7	5	73.985	69.83398	1.05945	1.0000
8	7	64.779	69.83398	0.92762	1.0000
7	4	45.745	69.83398	0.65506	1.0000
8	6	23.488	69.83398	0.33634	1.0000
12	11	17.145	69.83398	0.24551	1.0000
12	10	10.880	69.83398	0.15580	1.0000
8	3	-4.750	69.83398	-0.06802	1.0000
11	10	-6.260	69.83398	-0.08964	1.0000
5	4	-28.235	69.83398	-0.40432	1.0000
6	3	-28.243	69.83398	-0.40443	1.0000
12	9	-29.071	69.83398	-0.41629	1.0000
10	9	-39.956	69.83398	-0.57216	1.0000
7	6	-41.287	69.83398	-0.59121	1.0000
11	9	-46.221	69.83398	-0.66186	1.0000
9	5	-52.880	69.83398	-0.75722	1.0000
7	3	-69.534	69.83398	-0.99571	1.0000
9	4	-81.120	69.83398	-1.16161	1.0000
12	5	-81.956	69.83398	-1.17358	1.0000
10	5	-92.841	69.83398	-1.32945	1.0000
11	5	-99.105	69.83398	-1.41916	1.0000
12	4	-110.196	69.83398	-1.57797	1.0000
4	3	-115.284	69.83398	-1.65083	1.0000
10	4	-121.081	69.83398	-1.73384	1.0000
9	7	-126.870	69.83398	-1.81674	1.0000
11	4	-127.346	69.83398	-1.82355	1.0000
5	3	-143.525	69.83398	-2.05522	1.0000
12	7	-155.946	69.83398	-2.23310	1.0000
10	7	-166.831	69.83398	-2.38896	1.0000
9	6	-168.162	69.83398	-2.40802	1.0000
3	2	-170.174	69.83398	-2.43684	0.9779
11	7	-173.096	69.83398	-2.47867	0.8704
8	2	-174.929	69.83398	-2.50493	0.8083
9	8	-191.654	69.83398	-2.74443	0.4001

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
9	3	-196.409	69.83398	-2.81252	0.3244
12	6	-197.238	69.83398	-2.82438	0.3127
6	2	-198.422	69.83398	-2.84133	0.2965
10	6	-208.123	69.83398	-2.98025	0.1901
11	6	-214.387	69.83398	-3.06996	0.1413
12	8	-220.730	69.83398	-3.16079	0.1038
12	3	-225.485	69.83398	-3.22888	0.0820
10	8	-231.615	69.83398	-3.31665	0.0601
10	3	-236.370	69.83398	-3.38474	0.0470*
11	8	-237.880	69.83398	-3.40636	0.0435*
7	2	-239.713	69.83398	-3.43262	0.0395*
11	3	-242.635	69.83398	-3.47445	0.0338*
4	2	-285.463	69.83398	-4.08774	0.0029*
5	2	-313.703	69.83398	-4.49213	0.0005*
9	2	-366.588	69.83398	-5.24942	<.0001*
12	2	-395.664	69.83398	-5.66578	<.0001*
10	2	-406.549	69.83398	-5.82165	<.0001*
11	2	-412.814	69.83398	-5.91136	<.0001*

Continuous Isomodal Noise

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	160	130674	153680	816.71	-3.438
2	160	155701	153680	973.13	0.302
3	160	163195	153680	1019.97	1.422
4	160	166199	153680	1038.74	1.871
5	160	174772	153680	1092.33	3.152
6	160	155572	153680	972.32	0.283
7	160	163838	153680	1023.99	1.518

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
8	160	171255	153680	1070.34	2.626
9	160	141402	153680	883.76	-1.835
10	160	136734	153680	854.59	-2.532
11	160	142833	153680	892.71	-1.621
12	160	141987	153680	887.42	-1.747

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
47.7744	11	<.0001*

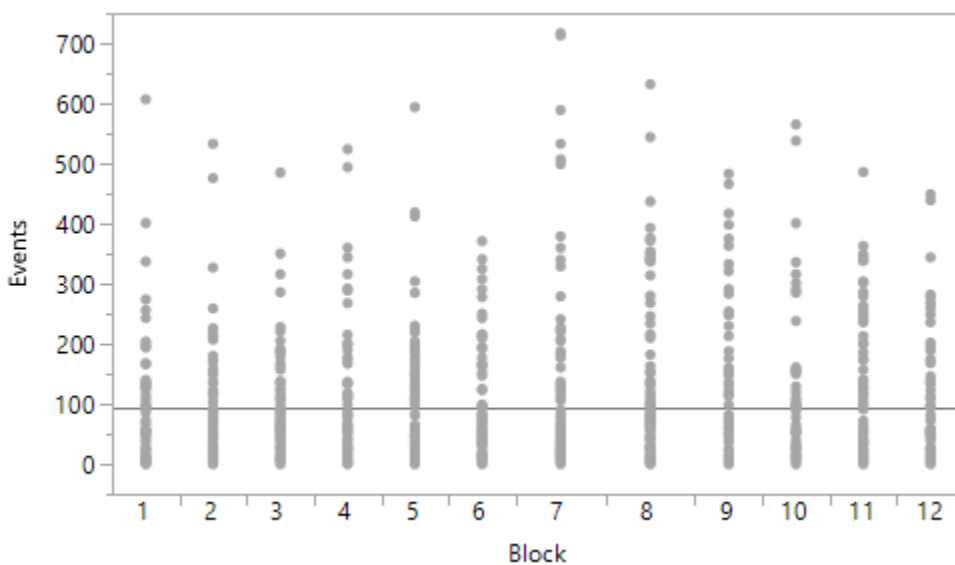
Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
5	1	275.609	61.77246	4.46169	0.0005*
8	1	253.625	61.77246	4.10579	0.0027*
4	1	222.028	61.77246	3.59429	0.0215*
7	1	207.272	61.77246	3.35541	0.0523
3	1	203.250	61.77246	3.29030	0.0661
2	1	156.416	61.77246	2.53213	0.7483
6	1	155.606	61.77246	2.51902	0.7767
5	2	119.188	61.77246	1.92946	1.0000
8	6	98.013	61.77246	1.58667	1.0000
8	2	97.203	61.77246	1.57357	1.0000
11	1	75.991	61.77246	1.23017	1.0000
5	3	72.353	61.77246	1.17128	1.0000
12	1	70.703	61.77246	1.14457	1.0000
9	1	67.047	61.77246	1.08538	1.0000
4	2	65.606	61.77246	1.06206	1.0000
5	4	53.575	61.77246	0.86730	1.0000
7	6	51.659	61.77246	0.83628	1.0000
7	2	50.850	61.77246	0.82318	1.0000
8	3	50.369	61.77246	0.81539	1.0000
3	2	46.828	61.77246	0.75807	1.0000
8	7	46.347	61.77246	0.75028	1.0000
11	10	38.112	61.77246	0.61698	1.0000
10	1	37.872	61.77246	0.61309	1.0000
12	10	32.825	61.77246	0.53139	1.0000
8	4	31.591	61.77246	0.51140	1.0000
4	3	18.772	61.77246	0.30389	1.0000
11	9	8.938	61.77246	0.14468	1.0000
7	3	4.016	61.77246	0.06501	1.0000
12	9	3.650	61.77246	0.05909	1.0000
6	2	-0.803	61.77246	-0.01300	1.0000
12	11	-5.281	61.77246	-0.08550	1.0000
7	4	-14.750	61.77246	-0.23878	1.0000
8	5	-21.978	61.77246	-0.35579	1.0000
10	9	-29.169	61.77246	-0.47220	1.0000
6	3	-47.637	61.77246	-0.77118	1.0000
6	4	-66.416	61.77246	-1.07517	1.0000
7	5	-68.331	61.77246	-1.10618	1.0000
11	6	-79.609	61.77246	-1.28875	1.0000

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
11	2	-80.419	61.77246	-1.30185	1.0000
12	6	-84.897	61.77246	-1.37435	1.0000
12	2	-85.706	61.77246	-1.38745	1.0000
9	6	-88.553	61.77246	-1.43354	1.0000
9	2	-89.362	61.77246	-1.44664	1.0000
10	6	-117.728	61.77246	-1.90584	1.0000
10	2	-118.537	61.77246	-1.91894	1.0000
6	5	-119.997	61.77246	-1.94256	1.0000
11	3	-127.253	61.77246	-2.06003	1.0000
11	7	-131.275	61.77246	-2.12514	1.0000
12	3	-132.541	61.77246	-2.14563	1.0000
9	3	-136.197	61.77246	-2.20482	1.0000
12	7	-136.563	61.77246	-2.21073	1.0000
9	7	-140.219	61.77246	-2.26992	1.0000
11	4	-146.031	61.77246	-2.36402	1.0000
12	4	-151.319	61.77246	-2.44961	0.9439
9	4	-154.975	61.77246	-2.50880	0.7995
10	3	-165.372	61.77246	-2.67711	0.4901
10	7	-169.394	61.77246	-2.74222	0.4028
11	8	-177.628	61.77246	-2.87552	0.2662
12	8	-182.916	61.77246	-2.96112	0.2023
10	4	-184.150	61.77246	-2.98110	0.1896
9	8	-186.572	61.77246	-3.02031	0.1667
11	5	-199.613	61.77246	-3.23142	0.0813
12	5	-204.900	61.77246	-3.31701	0.0601
9	5	-208.556	61.77246	-3.37620	0.0485*
10	8	-215.747	61.77246	-3.49261	0.0316*
10	5	-237.731	61.77246	-3.84850	0.0078*

Intermittent Crossmodal Noise

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	78	36865.5	38571.0	472.635	-0.708
2	78	38118.5	38571.0	488.699	-0.188
3	78	40234.5	38571.0	515.827	0.691
4	78	37044.5	38571.0	474.929	-0.634
5	78	40624.5	38571.0	520.827	0.852
6	78	40679.0	38571.0	521.526	0.875
7	104	53922.0	51428.0	518.481	0.910
8	104	52800.5	51428.0	507.697	0.501
9	78	38046.5	38571.0	487.776	-0.218
10	78	32717.0	38571.0	419.449	-2.431
11	78	41941.5	38571.0	537.712	1.399
12	78	35572.0	38571.0	456.051	-1.245

Oneway Test ChiSquare Approximation

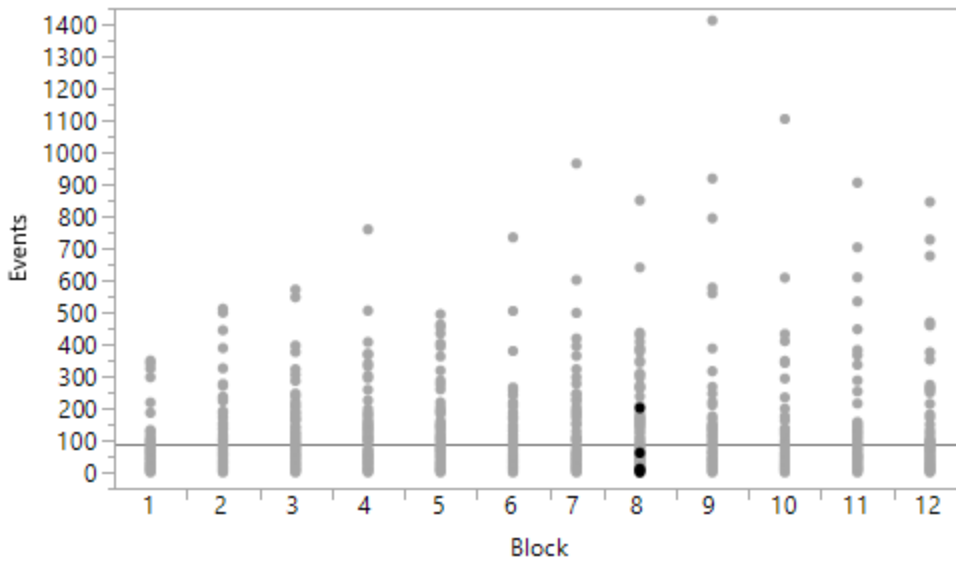
ChiSquare	DF	Prob>ChiSq
12.3629	11	0.3370

Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
11	10	118.250	45.49720	2.59906	0.6170
11	1	65.064	45.49720	1.43007	1.0000
11	4	62.769	45.49720	1.37963	1.0000
11	9	49.923	45.49720	1.09728	1.0000
11	2	49.000	45.49720	1.07699	1.0000
6	1	48.878	45.49720	1.07431	1.0000
5	1	48.179	45.49720	1.05895	1.0000
6	4	46.583	45.49720	1.02387	1.0000
5	4	45.885	45.49720	1.00852	1.0000
7	1	45.835	42.55874	1.07698	1.0000
7	4	43.540	42.55874	1.02306	1.0000
3	1	43.179	45.49720	0.94906	1.0000
12	10	36.590	45.49720	0.80422	1.0000
8	1	35.051	42.55874	0.82360	1.0000
6	2	32.814	45.49720	0.72123	1.0000
8	4	32.756	42.55874	0.76968	1.0000
5	2	32.115	45.49720	0.70588	1.0000
11	8	30.003	42.55874	0.70498	1.0000
7	2	29.771	42.55874	0.69952	1.0000
3	2	27.115	45.49720	0.59598	1.0000
11	3	21.872	45.49720	0.48073	1.0000
11	7	19.220	42.55874	0.45160	1.0000
8	2	18.987	42.55874	0.44614	1.0000
11	5	16.872	45.49720	0.37083	1.0000
11	6	16.173	45.49720	0.35547	1.0000
2	1	16.051	45.49720	0.35280	1.0000
9	1	15.128	45.49720	0.33251	1.0000
9	4	12.833	45.49720	0.28207	1.0000
6	3	5.686	45.49720	0.12497	1.0000
5	3	4.987	45.49720	0.10962	1.0000
7	3	2.643	42.55874	0.06209	1.0000

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
4	1	2.282	45.49720	0.05016	1.0000
6	5	0.686	45.49720	0.01508	1.0000
9	2	-0.910	45.49720	-0.02001	1.0000
7	5	-2.335	42.55874	-0.05486	1.0000
7	6	-3.034	42.55874	-0.07128	1.0000
8	3	-8.119	42.55874	-0.19076	1.0000
8	7	-10.774	39.40173	-0.27344	1.0000
8	5	-13.119	42.55874	-0.30825	1.0000
4	2	-13.756	45.49720	-0.30236	1.0000
8	6	-13.817	42.55874	-0.32466	1.0000
12	1	-16.571	45.49720	-0.36421	1.0000
12	4	-18.865	45.49720	-0.41465	1.0000
9	8	-19.910	42.55874	-0.46783	1.0000
9	3	-28.038	45.49720	-0.61627	1.0000
9	7	-30.694	42.55874	-0.72121	1.0000
12	9	-31.712	45.49720	-0.69700	1.0000
12	2	-32.635	45.49720	-0.71729	1.0000
9	5	-33.038	45.49720	-0.72616	1.0000
9	6	-33.737	45.49720	-0.74152	1.0000
4	3	-40.885	45.49720	-0.89862	1.0000
12	8	-51.635	42.55874	-1.21326	1.0000
10	1	-53.173	45.49720	-1.16871	1.0000
10	4	-55.468	45.49720	-1.21915	1.0000
12	3	-59.763	45.49720	-1.31355	1.0000
12	7	-62.418	42.55874	-1.46664	1.0000
12	5	-64.763	45.49720	-1.42345	1.0000
12	6	-65.462	45.49720	-1.43880	1.0000
10	9	-68.314	45.49720	-1.50150	1.0000
10	2	-69.237	45.49720	-1.52179	1.0000
12	11	-81.647	45.49720	-1.79456	1.0000
10	8	-88.237	42.55874	-2.07330	1.0000
10	3	-96.365	45.49720	-2.11805	1.0000
10	7	-99.021	42.55874	-2.32669	1.0000
10	5	-101.365	45.49720	-2.22795	1.0000
10	6	-102.064	45.49720	-2.24331	1.0000

Continuous Crossmodal Noise
Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	120	63898.0	84660.0	532.483	-4.871
2	120	85753.5	84660.0	714.613	0.256
3	120	96679.5	84660.0	805.663	2.820
4	120	86512.0	84660.0	720.933	0.434
5	120	91532.0	84660.0	762.767	1.612
6	120	86358.5	84660.0	719.654	0.398
7	90	70378.5	63495.0	781.983	1.843
8	120	96910.0	84660.0	807.583	2.874
9	120	81997.0	84660.0	683.308	-0.625
10	120	76367.5	84660.0	636.396	-1.946
11	120	83804.0	84660.0	698.367	-0.201
12	120	74564.5	84660.0	621.371	-2.369

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
51.4749	11	<.0001*

Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

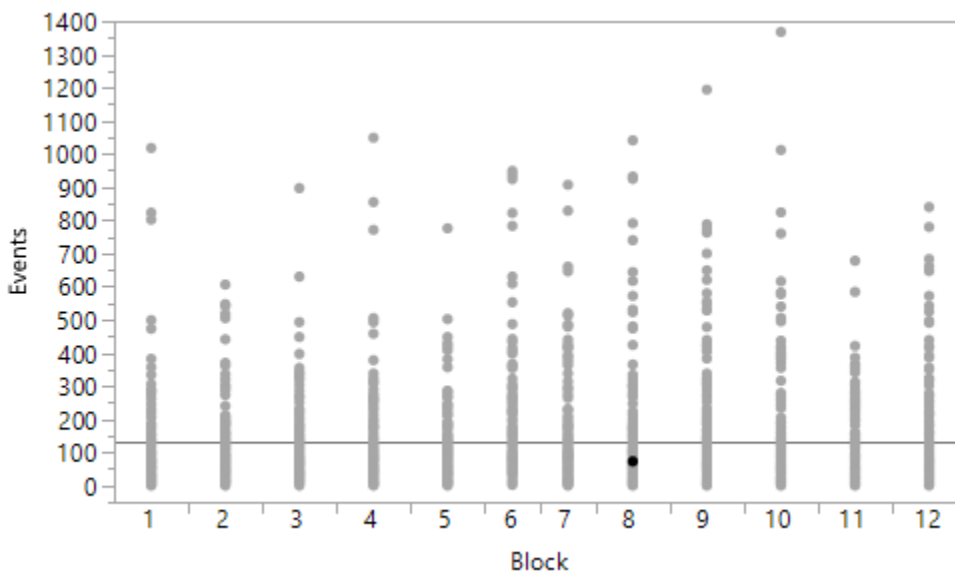
Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
8	1	275.092	52.51266	5.23858	<.0001*
3	1	273.171	52.51266	5.20200	<.0001*
7	1	249.490	56.72016	4.39862	0.0007*
5	1	230.275	52.51266	4.38513	0.0008*
4	1	188.442	52.51266	3.58850	0.0220*
6	1	187.163	52.51266	3.56414	0.0241*
2	1	182.121	52.51266	3.46813	0.0346*
11	1	165.875	52.51266	3.15876	0.1046
9	1	150.817	52.51266	2.87201	0.2692
10	1	103.904	52.51266	1.97865	1.0000
8	2	92.962	52.51266	1.77029	1.0000
3	2	91.042	52.51266	1.73371	1.0000

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
12	1	88.879	52.51266	1.69253	1.0000
8	6	87.921	52.51266	1.67428	1.0000
8	4	86.642	52.51266	1.64992	1.0000
7	2	67.361	56.72016	1.18760	1.0000
7	6	62.319	56.72016	1.09872	1.0000
11	10	61.962	52.51266	1.17995	1.0000
7	4	61.040	56.72016	1.07617	1.0000
5	2	48.146	52.51266	0.91684	1.0000
8	5	44.808	52.51266	0.85329	1.0000
5	4	41.825	52.51266	0.79647	1.0000
8	7	25.590	56.72016	0.45117	1.0000
7	5	19.207	56.72016	0.33863	1.0000
11	9	15.050	52.51266	0.28660	1.0000
4	2	6.313	52.51266	0.12021	1.0000
6	2	5.033	52.51266	0.09585	1.0000
8	3	1.913	52.51266	0.03642	1.0000
6	4	-1.271	52.51266	-0.02420	1.0000
12	10	-15.017	52.51266	-0.28596	1.0000
11	2	-16.238	52.51266	-0.30921	1.0000
11	6	-21.279	52.51266	-0.40522	1.0000
11	4	-22.558	52.51266	-0.42958	1.0000
7	3	-23.669	56.72016	-0.41730	1.0000
9	2	-31.296	52.51266	-0.59597	1.0000
9	6	-36.337	52.51266	-0.69198	1.0000
9	4	-37.617	52.51266	-0.71634	1.0000
5	3	-42.887	52.51266	-0.81671	1.0000
6	5	-43.104	52.51266	-0.82083	1.0000
10	9	-46.904	52.51266	-0.89320	1.0000
12	9	-61.929	52.51266	-1.17932	1.0000
11	5	-64.392	52.51266	-1.22621	1.0000
12	11	-76.987	52.51266	-1.46608	1.0000
10	2	-78.208	52.51266	-1.48932	1.0000
9	5	-79.450	52.51266	-1.51297	1.0000
10	6	-83.250	52.51266	-1.58533	1.0000
11	7	-83.607	56.72016	-1.47403	1.0000
10	4	-84.529	52.51266	-1.60969	1.0000
4	3	-84.721	52.51266	-1.61334	1.0000
6	3	-86.000	52.51266	-1.63770	1.0000
12	2	-93.233	52.51266	-1.77544	1.0000
12	6	-98.275	52.51266	-1.87145	1.0000
9	7	-98.665	56.72016	-1.73951	1.0000
12	4	-99.554	52.51266	-1.89581	1.0000
11	3	-107.288	52.51266	-2.04308	1.0000
11	8	-109.208	52.51266	-2.07966	1.0000
9	3	-122.346	52.51266	-2.32983	1.0000
9	8	-124.267	52.51266	-2.36641	1.0000
10	5	-126.363	52.51266	-2.40632	1.0000
12	5	-141.388	52.51266	-2.69245	0.4681
10	7	-145.578	56.72016	-2.56660	0.6778
12	7	-160.603	56.72016	-2.83149	0.3058
10	3	-169.258	52.51266	-3.22319	0.0837
10	8	-171.179	52.51266	-3.25977	0.0736

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
12	3	-184.283	52.51266	-3.50931	0.0297*
12	8	-186.204	52.51266	-3.54589	0.0258*

Intermittent Multimodal Noise

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	164	131689	154734	802.98	-3.460
2	164	171445	154734	1045.39	2.509
3	164	156406	154734	953.70	0.251
4	164	137651	154734	839.33	-2.565
5	164	147864	154734	901.61	-1.031
6	123	151043	116051	1227.99	5.995
7	123	126949	116051	1032.11	1.867
8	164	160391	154734	977.99	0.849
9	164	163490	154734	996.89	1.314
10	164	144467	154734	880.90	-1.541
11	164	137527	154734	838.58	-2.583
12	164	150521	154734	917.81	-0.632

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
71.4288	11	<.0001*

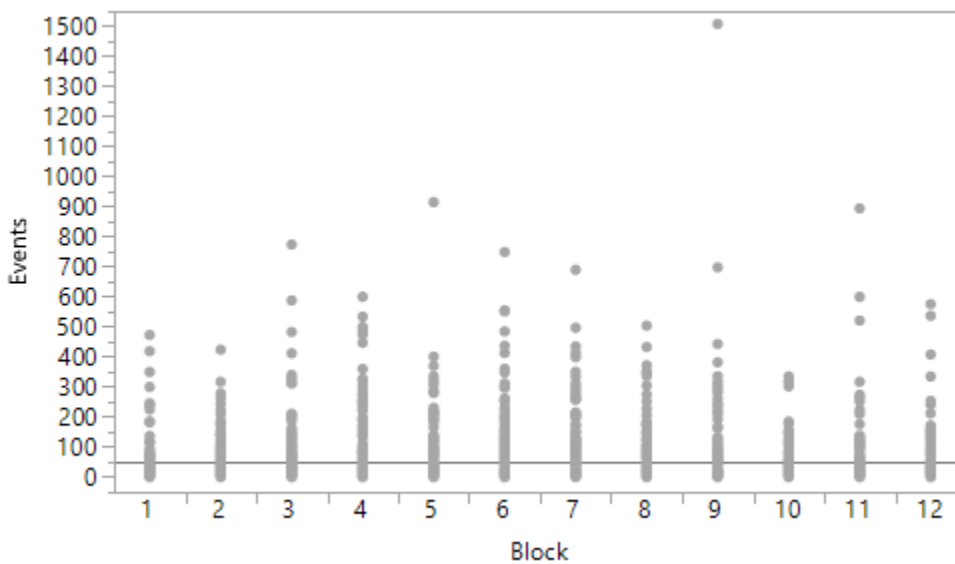
Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
6	1	425.003	64.92907	6.54565	<.0001*
6	4	388.652	64.92907	5.98580	<.0001*
6	5	326.378	64.92907	5.02669	<.0001*
6	3	274.290	64.92907	4.22445	0.0016*
2	1	242.405	60.11264	4.03252	0.0036*
7	1	229.117	64.92907	3.52873	0.0276*
9	1	193.899	60.11264	3.22560	0.0830
7	4	192.766	64.92907	2.96887	0.1973
6	2	182.591	64.92907	2.81217	0.3248
8	1	175.006	60.11264	2.91130	0.2376
9	4	157.549	60.11264	2.62089	0.5788
3	1	150.707	60.11264	2.50708	0.8034
8	4	138.655	60.11264	2.30659	1.0000
7	5	130.492	64.92907	2.00976	1.0000
12	1	114.823	60.11264	1.91013	1.0000
5	1	98.619	60.11264	1.64057	1.0000
9	5	95.274	60.11264	1.58493	1.0000
12	11	79.226	60.11264	1.31795	1.0000
12	4	78.473	60.11264	1.30543	1.0000
7	3	78.403	64.92907	1.20752	1.0000
10	1	77.909	60.11264	1.29604	1.0000
8	5	76.381	60.11264	1.27063	1.0000
5	4	62.268	60.11264	1.03586	1.0000
9	3	43.186	60.11264	0.71842	1.0000
10	4	41.558	60.11264	0.69133	1.0000
12	10	36.909	60.11264	0.61399	1.0000
4	1	36.345	60.11264	0.60461	1.0000
11	1	35.591	60.11264	0.59208	1.0000
8	3	24.293	60.11264	0.40412	1.0000
9	8	18.887	60.11264	0.31420	1.0000
12	5	16.198	60.11264	0.26946	1.0000
11	4	-0.747	60.11264	-0.01243	1.0000
7	2	-13.280	64.92907	-0.20454	1.0000
10	5	-20.704	60.11264	-0.34442	1.0000
9	7	-35.211	64.92907	-0.54231	1.0000
12	3	-35.878	60.11264	-0.59685	1.0000
11	10	-42.311	60.11264	-0.70386	1.0000
9	2	-48.500	60.11264	-0.80682	1.0000
5	3	-52.082	60.11264	-0.86641	1.0000
8	7	-54.105	64.92907	-0.83329	1.0000
12	8	-60.177	60.11264	-1.00107	1.0000
11	5	-63.021	60.11264	-1.04839	1.0000
8	2	-67.393	60.11264	-1.12112	1.0000
10	3	-72.793	60.11264	-1.21094	1.0000
12	9	-79.070	60.11264	-1.31537	1.0000
3	2	-91.692	60.11264	-1.52534	1.0000
10	8	-97.091	60.11264	-1.61516	1.0000
12	7	-114.288	64.92907	-1.76019	1.0000
4	3	-114.357	60.11264	-1.90237	1.0000
11	3	-115.110	60.11264	-1.91490	1.0000
10	9	-115.985	60.11264	-1.92946	1.0000
12	2	-127.576	60.11264	-2.12229	1.0000

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
11	8	-139.409	60.11264	-2.31912	1.0000
5	2	-143.780	60.11264	-2.39185	1.0000
10	7	-151.202	64.92907	-2.32873	1.0000
11	9	-158.302	60.11264	-2.63342	0.5579
10	2	-164.491	60.11264	-2.73638	0.4100
11	7	-193.519	64.92907	-2.98047	0.1900
7	6	-195.878	69.41210	-2.82196	0.3150
4	2	-206.055	60.11264	-3.42781	0.0402*
11	2	-206.808	60.11264	-3.44034	0.0383*
9	6	-231.098	64.92907	-3.55923	0.0245*
8	6	-249.991	64.92907	-3.85021	0.0078*
12	6	-310.174	64.92907	-4.77712	0.0001*
10	6	-347.088	64.92907	-5.34566	<.0001*
11	6	-389.405	64.92907	-5.99740	<.0001*

Continuous Multimodal Noise

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	184	180165	203228	979.16	-2.824
2	184	212115	203228	1152.80	1.088
3	184	227158	203228	1234.55	2.930
4	184	226859	203228	1232.93	2.894
5	184	216848	203228	1178.52	1.668
6	184	226289	203228	1229.83	2.824
7	184	229397	203228	1246.72	3.204
8	184	225135	203228	1223.56	2.683
9	184	173585	203228	943.39	-3.630
10	184	170839	203228	928.47	-3.966
11	184	169824	203228	922.96	-4.090

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
12	184	180525	203228	981.11	-2.780

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
98.7359	11	<.0001*

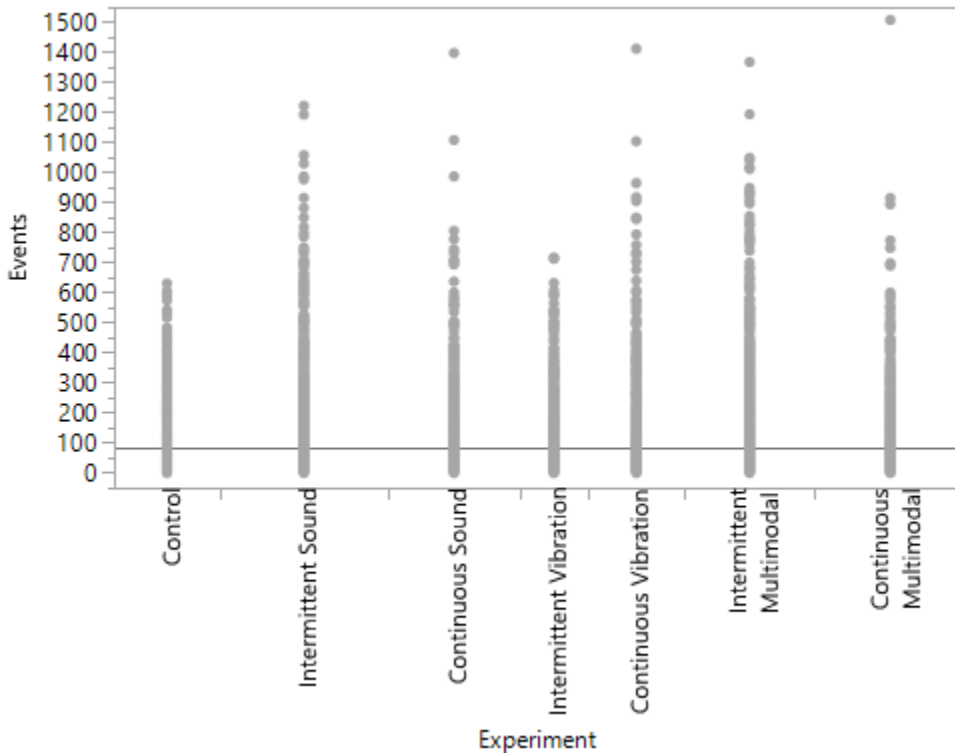
Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
7	1	267.557	65.55589	4.08136	0.0030*
3	1	255.391	65.55589	3.89578	0.0065*
4	1	253.764	65.55589	3.87095	0.0072*
6	1	250.666	65.55589	3.82370	0.0087*
8	1	244.394	65.55589	3.72803	0.0127*
5	1	199.359	65.55589	3.04105	0.1556
2	1	173.636	65.55589	2.64867	0.5333
7	2	93.916	65.55589	1.43261	1.0000
3	2	81.750	65.55589	1.24703	1.0000
4	2	80.122	65.55589	1.22220	1.0000
6	2	77.024	65.55589	1.17494	1.0000
8	2	70.753	65.55589	1.07927	1.0000
7	5	68.193	65.55589	1.04023	1.0000
12	11	58.152	65.55589	0.88706	1.0000
12	10	52.639	65.55589	0.80296	1.0000
6	5	51.302	65.55589	0.78256	1.0000
8	5	45.030	65.55589	0.68689	1.0000
12	9	37.715	65.55589	0.57531	1.0000
5	2	25.717	65.55589	0.39230	1.0000
7	6	16.886	65.55589	0.25758	1.0000
7	4	13.788	65.55589	0.21033	1.0000
7	3	12.160	65.55589	0.18550	1.0000
12	1	1.951	65.55589	0.02976	1.0000
4	3	-1.622	65.55589	-0.02475	1.0000
6	4	-3.092	65.55589	-0.04717	1.0000
6	3	-4.720	65.55589	-0.07200	1.0000
11	10	-5.508	65.55589	-0.08402	1.0000
8	6	-6.266	65.55589	-0.09559	1.0000
8	4	-9.364	65.55589	-0.14284	1.0000
8	3	-10.992	65.55589	-0.16767	1.0000
10	9	-14.918	65.55589	-0.22757	1.0000
11	9	-20.432	65.55589	-0.31167	1.0000
8	7	-23.158	65.55589	-0.35325	1.0000
9	1	-35.758	65.55589	-0.54546	1.0000
10	1	-50.682	65.55589	-0.77311	1.0000
5	4	-54.399	65.55589	-0.82982	1.0000
5	3	-56.027	65.55589	-0.85465	1.0000
11	1	-56.196	65.55589	-0.85722	1.0000
12	2	-171.679	65.55589	-2.61882	0.5823
12	5	-197.402	65.55589	-3.01120	0.1717
9	2	-209.399	65.55589	-3.19421	0.0925
10	2	-224.323	65.55589	-3.42186	0.0410*

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
11	2	-229.837	65.55589	-3.50597	0.0300*
9	5	-235.122	65.55589	-3.58659	0.0221*
12	8	-242.438	65.55589	-3.69818	0.0143*
12	6	-248.709	65.55589	-3.79385	0.0098*
10	5	-250.046	65.55589	-3.81424	0.0090*
12	4	-251.807	65.55589	-3.84111	0.0081*
12	3	-253.435	65.55589	-3.86593	0.0073*
11	5	-255.560	65.55589	-3.89835	0.0064*
12	7	-265.601	65.55589	-4.05151	0.0034*
9	8	-280.158	65.55589	-4.27357	0.0013*
9	6	-286.429	65.55589	-4.36924	0.0008*
9	4	-289.527	65.55589	-4.41649	0.0007*
9	3	-291.155	65.55589	-4.44132	0.0006*
10	8	-295.082	65.55589	-4.50122	0.0004*
11	8	-300.595	65.55589	-4.58533	0.0003*
10	6	-301.353	65.55589	-4.59689	0.0003*
9	7	-303.321	65.55589	-4.62690	0.0002*
10	4	-304.451	65.55589	-4.64415	0.0002*
10	3	-306.079	65.55589	-4.66898	0.0002*
11	6	-306.867	65.55589	-4.68100	0.0002*
11	4	-309.965	65.55589	-4.72825	0.0001*
11	3	-311.592	65.55589	-4.75308	0.0001*
10	7	-318.245	65.55589	-4.85455	<.0001*
11	7	-323.758	65.55589	-4.93866	<.0001*

Overall Comparisons

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
Control	1536	9486293	9520896	6175.97	-0.264
Intermittent Sound	2448	1.57e+7	1.52e+7	6420.02	3.429
Continuous Sound	1920	1.11e+7	1.19e+7	5803.90	-5.272
Intermittent Vibration	988	6501442	6124118	6580.41	3.507
Continuous Vibration	1410	9040366	8739885	6411.61	2.382
Intermittent Multimodal	1886	1.44e+7	1.17e+7	7629.21	18.913
Continuous Multimodal	2208	1.06e+7	1.37e+7	4782.66	-20.569

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
700.3284	6	<.0001*

Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

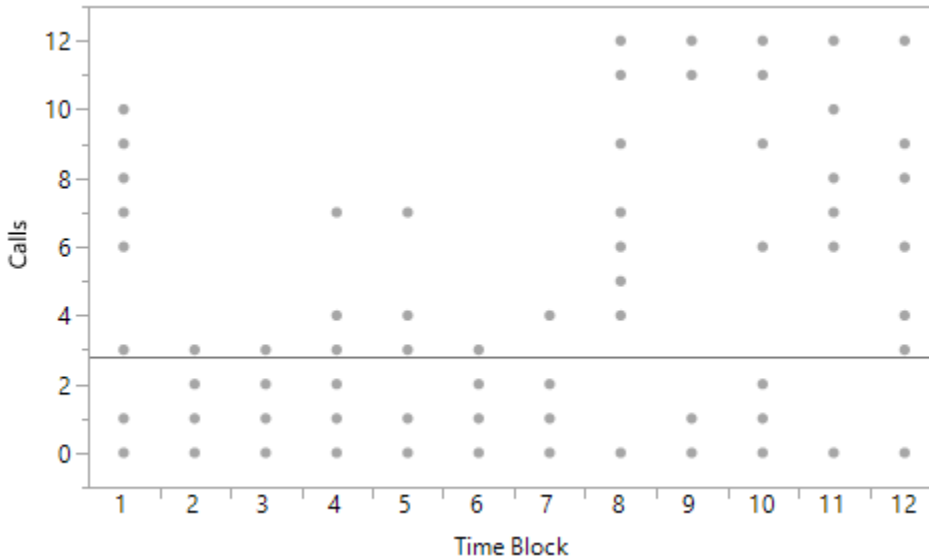
Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
Intermittent Multimodal	Continuous Sound	1825.31	115.6686	15.7805	<.0001*
Intermittent Multimodal	Control	1453.24	122.6241	11.8512	<.0001*
Intermittent Multimodal	Continuous Vibration	1217.60	125.6075	9.6937	<.0001*
Intermittent Multimodal	Intermittent Sound	1209.19	109.3126	11.0618	<.0001*
Intermittent Multimodal	Intermittent Vibration	1048.80	140.1188	7.4851	<.0001*
Intermittent Vibration	Continuous Sound	776.50	139.6917	5.5587	<.0001*
Continuous Vibration	Continuous Sound	607.70	125.1308	4.8565	<.0001*
Intermittent Vibration	Control	404.43	145.5033	2.7796	0.1143
Intermittent Sound	Control	244.05	116.1344	2.1014	0.7477

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
Continuous Vibration	Control	235.63	131.5872	1.7907	1.0000
Intermittent Vibration	Intermittent Sound	160.39	134.4760	1.1927	1.0000
Continuous Vibration	Intermittent Sound	-8.41	119.2802	-0.0705	1.0000
Continuous Vibration	Intermittent Vibration	-168.80	148.0263	-1.1403	1.0000
Continuous Sound	Control	-372.07	122.1358	-3.0463	0.0486*
Continuous Sound	Intermittent Sound	-616.11	108.7645	-5.6647	<.0001*
Continuous Multimodal	Continuous Sound	-1021.25	111.3325	-9.1729	<.0001*
Continuous Multimodal	Control	-1393.31	118.5428	-11.7537	<.0001*
Continuous Multimodal	Continuous Vibration	-1628.95	121.6263	-13.3931	<.0001*
Continuous Multimodal	Intermittent Sound	-1637.36	104.7137	-15.6366	<.0001*
Continuous Multimodal	Intermittent Vibration	-1797.75	136.5613	-13.1644	<.0001*
Continuous Multimodal	Intermittent Multimodal	-2846.55	111.8680	-25.4456	<.0001*

APPENDIX B: JMP RESULTS FOR CHAPTER 2

Control

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	56	21609.0	18844.0	385.875	2.224
2	56	14231.5	18844.0	254.134	-3.711
3	56	14394.5	18844.0	257.045	-3.580
4	56	17588.5	18844.0	314.080	-1.010
5	56	14453.5	18844.0	258.098	-3.532
6	56	14029.0	18844.0	250.518	-3.874
7	56	13794.0	18844.0	246.321	-4.063
8	56	17531.5	18844.0	313.063	-1.056
9	56	20216.0	18844.0	361.000	1.104
10	56	24293.0	18844.0	433.804	4.384
11	56	27074.0	18844.0	483.464	6.622
12	56	26913.5	18844.0	480.598	6.493

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
168.7858	11	<.0001*

Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

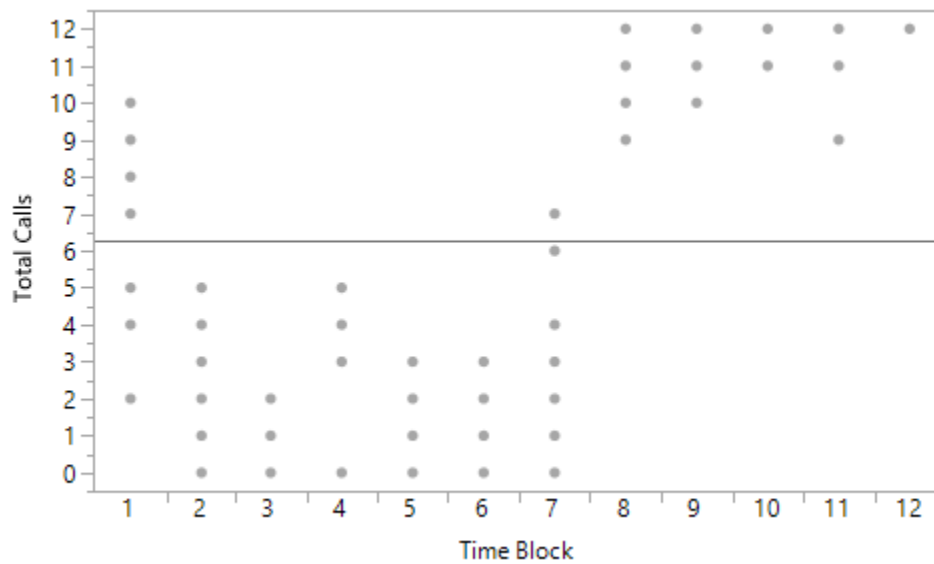
Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
11	7	237.125	32.78137	7.23353	<.0001*
12	7	234.259	32.78137	7.14610	<.0001*
11	6	232.929	32.78137	7.10552	<.0001*
12	6	230.063	32.78137	7.01809	<.0001*
11	2	229.313	32.78137	6.99521	<.0001*
12	2	226.446	32.78137	6.90778	<.0001*

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
11	3	226.402	32.78137	6.90642	<.0001*
11	5	225.348	32.78137	6.87428	<.0001*
12	3	223.536	32.78137	6.81899	<.0001*
12	5	222.482	32.78137	6.78685	<.0001*
10	7	187.464	32.78137	5.71862	<.0001*
10	6	183.268	32.78137	5.59061	<.0001*
10	2	179.652	32.78137	5.48030	<.0001*
10	3	176.741	32.78137	5.39151	<.0001*
10	5	175.688	32.78137	5.35937	<.0001*
11	8	170.384	32.78137	5.19758	<.0001*
11	4	169.366	32.78137	5.16653	<.0001*
12	8	167.518	32.78137	5.11015	<.0001*
12	4	166.500	32.78137	5.07910	<.0001*
11	9	122.446	32.78137	3.73524	0.0124*
10	8	120.723	32.78137	3.68268	0.0152*
10	4	119.705	32.78137	3.65163	0.0172*
12	9	119.580	32.78137	3.64781	0.0175*
9	7	114.661	32.78137	3.49774	0.0310*
9	6	110.464	32.78137	3.36973	0.0497*
9	2	106.848	32.78137	3.25942	0.0737
9	3	103.938	32.78137	3.17063	0.1004
9	5	102.884	32.78137	3.13849	0.1121
11	1	97.571	32.78137	2.97643	0.1925
12	1	94.705	32.78137	2.88900	0.2551
10	9	72.786	32.78137	2.22034	1.0000
8	7	66.723	32.78137	2.03540	1.0000
8	6	62.527	32.78137	1.90739	1.0000
4	2	59.929	32.78137	1.82813	1.0000
8	2	58.911	32.78137	1.79708	1.0000
4	3	57.018	32.78137	1.73934	1.0000
8	3	56.000	32.78137	1.70829	1.0000
8	5	54.946	32.78137	1.67615	1.0000
11	10	49.643	32.78137	1.51436	1.0000
9	8	47.920	32.78137	1.46180	1.0000
10	1	47.911	32.78137	1.46152	1.0000
9	4	46.902	32.78137	1.43075	1.0000
12	10	46.777	32.78137	1.42693	1.0000
5	2	3.946	32.78137	0.12039	1.0000
3	2	2.893	32.78137	0.08825	1.0000
5	3	1.036	32.78137	0.03159	1.0000
8	4	-1.000	32.78137	-0.03051	1.0000
12	11	-2.848	32.78137	-0.08689	1.0000
6	2	-3.598	32.78137	-0.10976	1.0000
7	6	-4.179	32.78137	-0.12747	1.0000
6	3	-6.509	32.78137	-0.19856	1.0000
6	5	-7.563	32.78137	-0.23070	1.0000
7	2	-7.795	32.78137	-0.23778	1.0000
7	3	-10.705	32.78137	-0.32657	1.0000
7	5	-11.759	32.78137	-0.35871	1.0000
9	1	-24.857	32.78137	-0.75827	1.0000
5	4	-55.964	32.78137	-1.70720	1.0000
6	4	-63.545	32.78137	-1.93844	1.0000

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
7	4	-67.741	32.78137	-2.06645	1.0000
4	1	-71.777	32.78137	-2.18956	1.0000
8	1	-72.795	32.78137	-2.22061	1.0000
5	1	-127.759	32.78137	-3.89730	0.0064*
3	1	-128.813	32.78137	-3.92944	0.0056*
2	1	-131.723	32.78137	-4.01823	0.0039*
6	1	-135.339	32.78137	-4.12854	0.0024*
7	1	-139.536	32.78137	-4.25656	0.0014*

Intermittent Isomodal Noise

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	80	39368.5	36520.0	492.106	1.295
2	72	22199.0	32868.0	308.319	-5.088
3	76	14407.5	34694.0	189.572	-9.440
4	76	13980.5	34694.0	183.954	-9.638
5	76	13534.5	34694.0	178.086	-9.846
6	76	16737.0	34694.0	220.224	-8.356
7	76	21742.0	34694.0	286.079	-6.027
8	76	50867.5	34694.0	669.309	7.526
9	76	54774.5	34694.0	720.717	9.344
10	76	55366.0	34694.0	728.500	9.619
11	76	55097.0	34694.0	724.961	9.494
12	76	58254.0	34694.0	766.500	10.963

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
787.9567	11	<.0001*

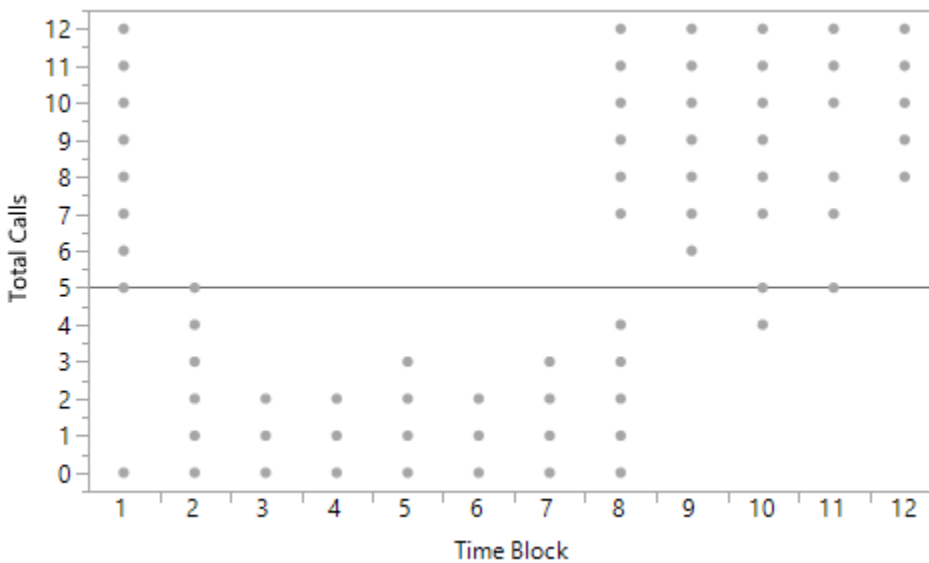
Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
12	5	588.401	41.76754	14.0875	<.0001*
12	4	582.533	41.76754	13.9470	<.0001*
12	3	576.914	41.76754	13.8125	<.0001*
10	5	550.401	41.76754	13.1777	<.0001*
11	5	546.862	41.76754	13.0930	<.0001*
12	6	546.263	41.76754	13.0787	<.0001*
10	4	544.533	41.76754	13.0372	<.0001*
9	5	542.618	41.76754	12.9914	<.0001*
11	4	540.993	41.76754	12.9525	<.0001*
10	3	538.914	41.76754	12.9027	<.0001*
9	4	536.750	41.76754	12.8509	<.0001*
11	3	535.375	41.76754	12.8180	<.0001*
9	3	531.132	41.76754	12.7164	<.0001*
10	6	508.263	41.76754	12.1689	<.0001*
11	6	504.724	41.76754	12.0841	<.0001*
9	6	500.480	41.76754	11.9825	<.0001*
8	5	491.211	41.76754	11.7606	<.0001*
8	4	485.342	41.76754	11.6201	<.0001*
12	7	480.408	41.76754	11.5019	<.0001*
8	3	479.724	41.76754	11.4856	<.0001*
12	2	458.167	42.34367	10.8202	<.0001*
8	6	449.072	41.76754	10.7517	<.0001*
10	7	442.408	41.76754	10.5921	<.0001*
11	7	438.868	41.76754	10.5074	<.0001*
9	7	434.625	41.76754	10.4058	<.0001*
10	2	420.167	42.34367	9.9228	<.0001*
11	2	416.628	42.34367	9.8392	<.0001*
9	2	412.384	42.34367	9.7390	<.0001*
8	7	383.217	41.76754	9.1750	<.0001*
8	2	360.976	42.34367	8.5249	<.0001*
12	1	274.381	41.24214	6.6529	<.0001*
10	1	236.381	41.24214	5.7315	<.0001*
11	1	232.841	41.24214	5.6457	<.0001*
9	1	228.598	41.24214	5.5428	<.0001*
8	1	177.190	41.24214	4.2963	0.0011*
7	5	107.980	41.76754	2.5853	0.6422
7	4	102.112	41.76754	2.4448	0.9566
12	8	97.178	41.76754	2.3266	1.0000
7	3	96.493	41.76754	2.3102	1.0000
7	6	65.842	41.76754	1.5764	1.0000
10	8	59.178	41.76754	1.4168	1.0000
11	8	55.638	41.76754	1.3321	1.0000
9	8	51.395	41.76754	1.2305	1.0000
12	9	45.770	41.76754	1.0958	1.0000
6	5	42.125	41.76754	1.0086	1.0000
12	11	41.526	41.76754	0.9942	1.0000
12	10	37.987	41.76754	0.9095	1.0000

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
6	4	36.257	41.76754	0.8681	1.0000
6	3	30.638	41.76754	0.7335	1.0000
10	9	7.770	41.76754	0.1860	1.0000
11	9	4.230	41.76754	0.1013	1.0000
11	10	-3.526	41.76754	-0.0844	1.0000
4	3	-5.605	41.76754	-0.1342	1.0000
5	4	-5.855	41.76754	-0.1402	1.0000
5	3	-11.474	41.76754	-0.2747	1.0000
7	2	-22.227	42.34367	-0.5249	1.0000
6	2	-88.082	42.34367	-2.0802	1.0000
3	2	-118.734	42.34367	-2.8040	0.3331
4	2	-124.352	42.34367	-2.9367	0.2189
5	2	-130.220	42.34367	-3.0753	0.1388
2	1	-183.774	41.82551	-4.3938	0.0007*
7	1	-206.014	41.24214	-4.9952	<.0001*
6	1	-271.870	41.24214	-6.5920	<.0001*
3	1	-302.521	41.24214	-7.3352	<.0001*
4	1	-308.139	41.24214	-7.4715	<.0001*
5	1	-314.008	41.24214	-7.6138	<.0001*

Continuous Isomodal Noise

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	80	44196.5	38440.0	552.456	2.495
2	80	29515.0	38440.0	368.938	-3.868
3	80	19486.5	38440.0	243.581	-8.215
4	80	18767.0	38440.0	234.588	-8.527
5	80	17984.0	38440.0	224.800	-8.867

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
6	80	19189.0	38440.0	239.863	-8.344
7	80	19843.5	38440.0	248.044	-8.061
8	80	39665.0	38440.0	495.813	0.531
9	80	58723.5	38440.0	734.044	8.792
10	80	64041.5	38440.0	800.519	11.097
11	80	64700.0	38440.0	808.750	11.382
12	80	65168.5	38440.0	814.606	11.585

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
769.2103	11	<.0001*

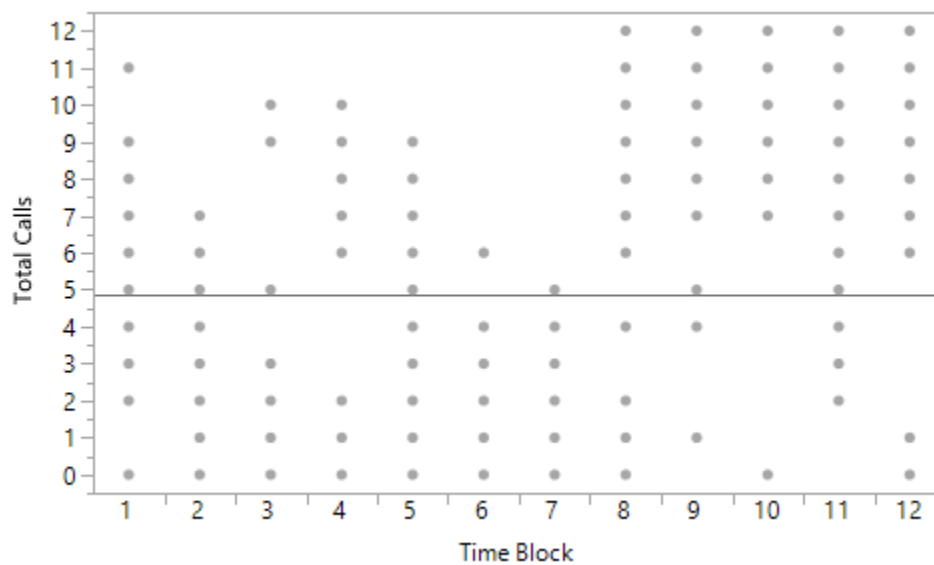
Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
12	5	589.794	42.59671	13.8460	<.0001*
11	5	583.938	42.59671	13.7085	<.0001*
12	4	580.006	42.59671	13.6162	<.0001*
10	5	575.706	42.59671	13.5153	<.0001*
12	6	574.731	42.59671	13.4924	<.0001*
11	4	574.150	42.59671	13.4787	<.0001*
12	3	571.013	42.59671	13.4051	<.0001*
11	6	568.875	42.59671	13.3549	<.0001*
12	7	566.550	42.59671	13.3003	<.0001*
10	4	565.919	42.59671	13.2855	<.0001*
11	3	565.156	42.59671	13.2676	<.0001*
11	7	560.694	42.59671	13.1628	<.0001*
10	6	560.644	42.59671	13.1617	<.0001*
10	3	556.925	42.59671	13.0744	<.0001*
10	7	552.463	42.59671	12.9696	<.0001*
9	5	509.231	42.59671	11.9547	<.0001*
9	4	499.444	42.59671	11.7249	<.0001*
9	6	494.169	42.59671	11.6011	<.0001*
9	3	490.450	42.59671	11.5138	<.0001*
9	7	485.988	42.59671	11.4090	<.0001*
12	2	445.656	42.59671	10.4622	<.0001*
11	2	439.800	42.59671	10.3247	<.0001*
10	2	431.569	42.59671	10.1315	<.0001*
9	2	365.094	42.59671	8.5709	<.0001*
12	8	318.781	42.59671	7.4837	<.0001*
11	8	312.925	42.59671	7.3462	<.0001*
10	8	304.694	42.59671	7.1530	<.0001*
8	5	271.000	42.59671	6.3620	<.0001*
12	1	262.138	42.59671	6.1539	<.0001*
8	4	261.213	42.59671	6.1322	<.0001*
11	1	256.281	42.59671	6.0165	<.0001*
8	6	255.938	42.59671	6.0084	<.0001*
8	3	252.219	42.59671	5.9211	<.0001*
10	1	248.050	42.59671	5.8232	<.0001*
8	7	247.756	42.59671	5.8163	<.0001*
9	8	238.219	42.59671	5.5924	<.0001*
9	1	181.575	42.59671	4.2627	0.0013*
8	2	126.862	42.59671	2.9782	0.1914

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
12	9	80.550	42.59671	1.8910	1.0000
11	9	74.694	42.59671	1.7535	1.0000
10	9	66.463	42.59671	1.5603	1.0000
7	5	23.231	42.59671	0.5454	1.0000
6	5	15.050	42.59671	0.3533	1.0000
12	10	14.075	42.59671	0.3304	1.0000
7	4	13.444	42.59671	0.3156	1.0000
11	10	8.219	42.59671	0.1929	1.0000
7	6	8.169	42.59671	0.1918	1.0000
12	11	5.844	42.59671	0.1372	1.0000
6	4	5.262	42.59671	0.1235	1.0000
7	3	4.450	42.59671	0.1045	1.0000
6	3	-3.706	42.59671	-0.0870	1.0000
4	3	-8.981	42.59671	-0.2108	1.0000
5	4	-9.775	42.59671	-0.2295	1.0000
5	3	-18.769	42.59671	-0.4406	1.0000
8	1	-56.631	42.59671	-1.3295	1.0000
7	2	-120.881	42.59671	-2.8378	0.2998
3	2	-125.344	42.59671	-2.9426	0.2148
6	2	-129.062	42.59671	-3.0299	0.1615
4	2	-134.338	42.59671	-3.1537	0.1064
5	2	-144.125	42.59671	-3.3835	0.0472*
2	1	-183.506	42.59671	-4.3080	0.0011*
7	1	-304.400	42.59671	-7.1461	<.0001*
3	1	-308.863	42.59671	-7.2509	<.0001*
6	1	-312.581	42.59671	-7.3382	<.0001*
4	1	-317.856	42.59671	-7.4620	<.0001*
5	1	-327.644	42.59671	-7.6918	<.0001*

Intermittent Crossmodal Noise

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	80	42526.5	38440.0	531.581	1.742
2	80	28922.5	38440.0	361.531	-4.058
3	80	23958.0	38440.0	299.475	-6.174
4	80	19779.0	38440.0	247.238	-7.956
5	80	20057.0	38440.0	250.713	-7.837
6	80	18169.5	38440.0	227.119	-8.642
7	80	20170.5	38440.0	252.131	-7.789
8	80	49404.5	38440.0	617.556	4.674
9	80	58209.0	38440.0	727.613	8.428
10	80	65244.5	38440.0	815.556	11.428
11	80	54249.0	38440.0	678.113	6.740
12	80	60590.0	38440.0	757.375	9.443

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
619.4811	11	<.0001*

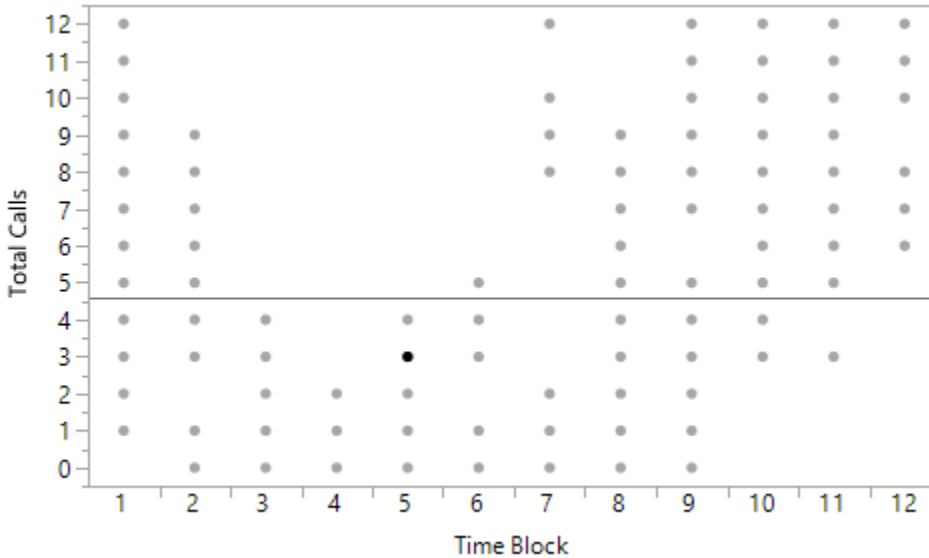
Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
10	6	588.425	43.30722	13.5872	<.0001*
10	4	568.306	43.30722	13.1227	<.0001*
10	5	564.831	43.30722	13.0424	<.0001*
10	7	563.413	43.30722	13.0097	<.0001*
12	6	530.244	43.30722	12.2438	<.0001*
10	3	516.069	43.30722	11.9165	<.0001*
12	4	510.125	43.30722	11.7792	<.0001*
12	5	506.650	43.30722	11.6990	<.0001*
12	7	505.231	43.30722	11.6662	<.0001*
9	6	500.481	43.30722	11.5565	<.0001*
9	4	480.363	43.30722	11.0920	<.0001*
9	5	476.888	43.30722	11.0117	<.0001*
9	7	475.469	43.30722	10.9790	<.0001*
12	3	457.888	43.30722	10.5730	<.0001*
10	2	454.013	43.30722	10.4835	<.0001*
11	6	450.981	43.30722	10.4135	<.0001*
11	4	430.863	43.30722	9.9490	<.0001*
9	3	428.125	43.30722	9.8858	<.0001*
11	5	427.388	43.30722	9.8687	<.0001*
11	7	425.969	43.30722	9.8360	<.0001*
12	2	395.831	43.30722	9.1401	<.0001*
8	6	390.425	43.30722	9.0152	<.0001*
11	3	378.625	43.30722	8.7428	<.0001*
8	4	370.306	43.30722	8.5507	<.0001*
8	5	366.831	43.30722	8.4704	<.0001*
9	2	366.069	43.30722	8.4528	<.0001*
8	7	365.413	43.30722	8.4377	<.0001*
8	3	318.069	43.30722	7.3445	<.0001*
11	2	316.569	43.30722	7.3098	<.0001*
10	1	283.963	43.30722	6.5569	<.0001*

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
8	2	256.012	43.30722	5.9115	<.0001*
12	1	225.781	43.30722	5.2135	<.0001*
10	8	197.987	43.30722	4.5717	0.0003*
9	1	196.019	43.30722	4.5262	0.0004*
11	1	146.519	43.30722	3.3832	0.0473*
12	8	139.806	43.30722	3.2282	0.0822
9	8	110.044	43.30722	2.5410	0.7295
10	9	87.931	43.30722	2.0304	1.0000
8	1	85.962	43.30722	1.9849	1.0000
12	11	79.250	43.30722	1.8299	1.0000
11	8	60.544	43.30722	1.3980	1.0000
12	9	29.750	43.30722	0.6870	1.0000
7	6	25.000	43.30722	0.5773	1.0000
7	4	4.881	43.30722	0.1127	1.0000
5	4	3.463	43.30722	0.0800	1.0000
7	5	1.406	43.30722	0.0325	1.0000
6	4	-20.106	43.30722	-0.4643	1.0000
6	5	-23.581	43.30722	-0.5445	1.0000
7	3	-47.331	43.30722	-1.0929	1.0000
5	3	-48.750	43.30722	-1.1257	1.0000
11	9	-49.488	43.30722	-1.1427	1.0000
4	3	-52.225	43.30722	-1.2059	1.0000
12	10	-58.169	43.30722	-1.3432	1.0000
3	2	-62.044	43.30722	-1.4326	1.0000
6	3	-72.344	43.30722	-1.6705	1.0000
7	2	-109.388	43.30722	-2.5258	0.7618
5	2	-110.806	43.30722	-2.5586	0.6936
4	2	-114.281	43.30722	-2.6388	0.5490
6	2	-134.400	43.30722	-3.1034	0.1263
11	10	-137.431	43.30722	-3.1734	0.0994
2	1	-170.038	43.30722	-3.9263	0.0057*
3	1	-232.094	43.30722	-5.3592	<.0001*
7	1	-279.438	43.30722	-6.4524	<.0001*
5	1	-280.856	43.30722	-6.4852	<.0001*
4	1	-284.331	43.30722	-6.5654	<.0001*
6	1	-304.450	43.30722	-7.0300	<.0001*

Continuous Crossmodal Noise

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	80	53132.0	38440.0	664.150	6.353
2	80	28896.0	38440.0	361.200	-4.127
3	80	24916.0	38440.0	311.450	-5.848
4	80	18101.5	38440.0	226.269	-8.795
5	80	16994.5	38440.0	212.431	-9.274
6	80	18853.0	38440.0	235.663	-8.470
7	80	24969.0	38440.0	312.113	-5.825
8	80	33397.5	38440.0	417.469	-2.180
9	80	54446.5	38440.0	680.581	6.922
10	80	59641.0	38440.0	745.513	9.168
11	80	60933.5	38440.0	761.669	9.727
12	80	66999.5	38440.0	837.494	12.351

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
682.5196	11	<.0001*

Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

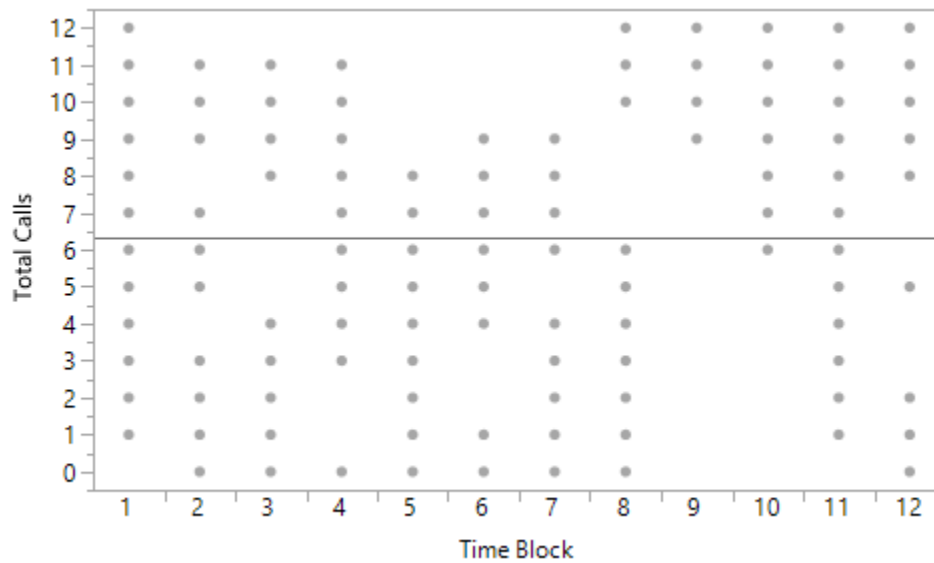
Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
12	5	625.050	42.69498	14.6399	<.0001*
12	4	611.213	42.69498	14.3158	<.0001*
12	6	601.819	42.69498	14.0958	<.0001*
11	5	549.225	42.69498	12.8639	<.0001*
11	4	535.388	42.69498	12.5398	<.0001*
10	5	533.069	42.69498	12.4855	<.0001*
12	3	526.031	42.69498	12.3207	<.0001*
11	6	525.994	42.69498	12.3198	<.0001*

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
12	7	525.369	42.69498	12.3052	<.0001*
10	4	519.231	42.69498	12.1614	<.0001*
10	6	509.838	42.69498	11.9414	<.0001*
12	2	476.281	42.69498	11.1554	<.0001*
9	5	468.138	42.69498	10.9647	<.0001*
9	4	454.300	42.69498	10.6406	<.0001*
11	3	450.206	42.69498	10.5447	<.0001*
11	7	449.544	42.69498	10.5292	<.0001*
9	6	444.906	42.69498	10.4206	<.0001*
10	3	434.050	42.69498	10.1663	<.0001*
10	7	433.388	42.69498	10.1508	<.0001*
12	8	420.013	42.69498	9.8375	<.0001*
11	2	400.456	42.69498	9.3795	<.0001*
10	2	384.300	42.69498	9.0011	<.0001*
9	3	369.119	42.69498	8.6455	<.0001*
9	7	368.456	42.69498	8.6300	<.0001*
11	8	344.188	42.69498	8.0615	<.0001*
10	8	328.031	42.69498	7.6831	<.0001*
9	2	319.369	42.69498	7.4802	<.0001*
9	8	263.100	42.69498	6.1623	<.0001*
8	5	205.025	42.69498	4.8021	0.0001*
8	4	191.188	42.69498	4.4780	0.0005*
8	6	181.794	42.69498	4.2580	0.0014*
12	1	173.331	42.69498	4.0598	0.0032*
12	9	156.900	42.69498	3.6749	0.0157*
8	3	106.006	42.69498	2.4829	0.8602
8	7	105.344	42.69498	2.4674	0.8984
7	5	99.669	42.69498	2.3344	1.0000
11	1	97.506	42.69498	2.2838	1.0000
12	10	91.969	42.69498	2.1541	1.0000
7	4	85.831	42.69498	2.0103	1.0000
10	1	81.350	42.69498	1.9054	1.0000
11	9	81.075	42.69498	1.8989	1.0000
7	6	76.438	42.69498	1.7903	1.0000
12	11	75.813	42.69498	1.7757	1.0000
10	9	64.919	42.69498	1.5205	1.0000
8	2	56.256	42.69498	1.3176	1.0000
6	5	23.219	42.69498	0.5438	1.0000
9	1	16.419	42.69498	0.3846	1.0000
11	10	16.144	42.69498	0.3781	1.0000
6	4	9.381	42.69498	0.2197	1.0000
7	3	0.650	42.69498	0.0152	1.0000
5	4	-13.825	42.69498	-0.3238	1.0000
7	2	-49.075	42.69498	-1.1494	1.0000
3	2	-49.738	42.69498	-1.1649	1.0000
6	3	-75.775	42.69498	-1.7748	1.0000
4	3	-85.169	42.69498	-1.9948	1.0000
5	3	-99.006	42.69498	-2.3189	1.0000
6	2	-125.525	42.69498	-2.9400	0.2166
4	2	-134.919	42.69498	-3.1601	0.1041
5	2	-148.756	42.69498	-3.4842	0.0326*
8	1	-246.669	42.69498	-5.7775	<.0001*

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
2	1	-302.938	42.69498	-7.0954	<.0001*
7	1	-352.025	42.69498	-8.2451	<.0001*
3	1	-352.688	42.69498	-8.2606	<.0001*
6	1	-428.475	42.69498	-10.0357	<.0001*
4	1	-437.869	42.69498	-10.2557	<.0001*
5	1	-451.706	42.69498	-10.5798	<.0001*

Intermittent Multimodal Noise

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	80	47195.5	38440.0	589.944	3.727
2	80	28176.0	38440.0	352.200	-4.369
3	80	29850.0	38440.0	373.125	-3.657
4	80	23065.0	38440.0	288.313	-6.545
5	80	21139.0	38440.0	264.238	-7.365
6	80	19839.5	38440.0	247.994	-7.918
7	80	22872.5	38440.0	285.906	-6.627
8	80	43881.5	38440.0	548.519	2.316
9	80	60571.0	38440.0	757.138	9.421
10	80	59003.0	38440.0	737.538	8.753
11	80	47389.0	38440.0	592.363	3.809
12	80	58298.0	38440.0	728.725	8.453

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
464.5394	11	<.0001*

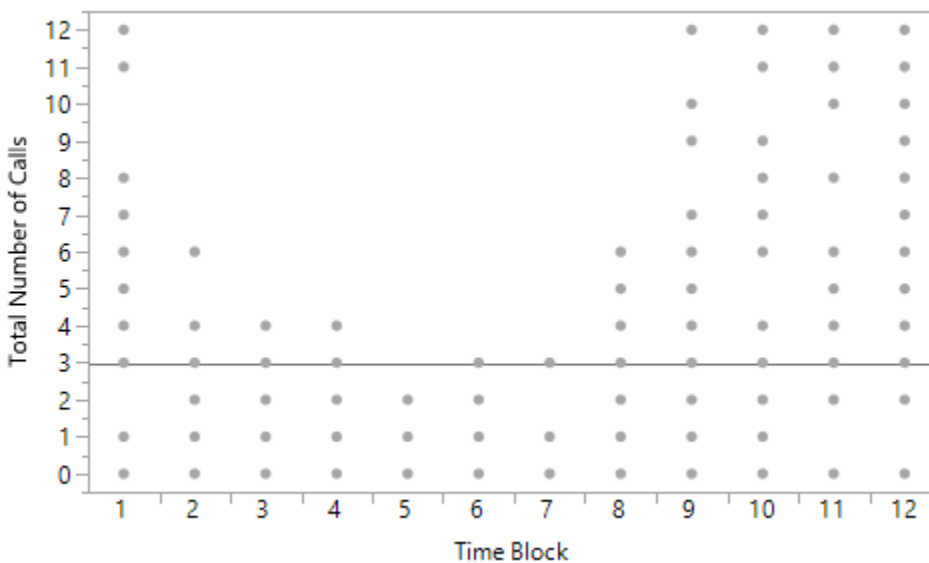
Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
9	6	509.131	43.37309	11.7384	<.0001*
9	5	492.888	43.37309	11.3639	<.0001*
10	6	489.531	43.37309	11.2865	<.0001*
12	6	480.719	43.37309	11.0833	<.0001*
10	5	473.288	43.37309	10.9120	<.0001*
9	7	471.219	43.37309	10.8643	<.0001*
9	4	468.813	43.37309	10.8088	<.0001*
12	5	464.475	43.37309	10.7088	<.0001*
10	7	451.619	43.37309	10.4124	<.0001*
10	4	449.213	43.37309	10.3569	<.0001*
12	7	442.806	43.37309	10.2092	<.0001*
12	4	440.400	43.37309	10.1538	<.0001*
9	2	404.925	43.37309	9.3359	<.0001*
10	2	385.325	43.37309	8.8840	<.0001*
9	3	384.000	43.37309	8.8534	<.0001*
12	2	376.513	43.37309	8.6808	<.0001*
10	3	364.400	43.37309	8.4015	<.0001*
12	3	355.588	43.37309	8.1983	<.0001*
11	6	344.356	43.37309	7.9394	<.0001*
11	5	328.113	43.37309	7.5649	<.0001*
11	7	306.444	43.37309	7.0653	<.0001*
11	4	304.038	43.37309	7.0098	<.0001*
8	6	300.513	43.37309	6.9285	<.0001*
8	5	284.269	43.37309	6.5540	<.0001*
8	7	262.600	43.37309	6.0544	<.0001*
8	4	260.194	43.37309	5.9990	<.0001*
11	2	240.150	43.37309	5.5368	<.0001*
11	3	219.225	43.37309	5.0544	<.0001*
9	8	208.606	43.37309	4.8096	<.0001*
8	2	196.306	43.37309	4.5260	0.0004*
10	8	189.006	43.37309	4.3577	0.0009*
12	8	180.194	43.37309	4.1545	0.0022*
8	3	175.381	43.37309	4.0435	0.0035*
9	1	167.181	43.37309	3.8545	0.0077*
10	1	147.581	43.37309	3.4026	0.0441*
12	1	138.769	43.37309	3.1994	0.0909
12	11	136.350	43.37309	3.1437	0.1101
11	8	43.831	43.37309	1.0106	1.0000
7	6	37.900	43.37309	0.8738	1.0000
7	5	21.656	43.37309	0.4993	1.0000
3	2	20.912	43.37309	0.4822	1.0000
11	1	2.406	43.37309	0.0555	1.0000
7	4	-2.394	43.37309	-0.0552	1.0000
12	10	-8.800	43.37309	-0.2029	1.0000
6	5	-16.231	43.37309	-0.3742	1.0000
10	9	-19.587	43.37309	-0.4516	1.0000
5	4	-24.063	43.37309	-0.5548	1.0000
12	9	-28.400	43.37309	-0.6548	1.0000
6	4	-40.306	43.37309	-0.9293	1.0000

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
8	1	-41.413	43.37309	-0.9548	1.0000
4	2	-63.875	43.37309	-1.4727	1.0000
7	2	-66.281	43.37309	-1.5282	1.0000
4	3	-84.800	43.37309	-1.9551	1.0000
7	3	-87.206	43.37309	-2.0106	1.0000
5	2	-87.950	43.37309	-2.0278	1.0000
6	2	-104.194	43.37309	-2.4023	1.0000
5	3	-108.875	43.37309	-2.5102	0.7964
6	3	-125.119	43.37309	-2.8847	0.2586
11	10	-145.163	43.37309	-3.3468	0.0539
11	9	-164.763	43.37309	-3.7987	0.0096*
3	1	-216.806	43.37309	-4.9986	<.0001*
2	1	-237.731	43.37309	-5.4811	<.0001*
4	1	-301.619	43.37309	-6.9541	<.0001*
7	1	-304.025	43.37309	-7.0095	<.0001*
5	1	-325.694	43.37309	-7.5091	<.0001*
6	1	-341.938	43.37309	-7.8836	<.0001*

Continuous Multimodal Noise

Oneway Analysis of Events by Block



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
1	80	57434.5	38440.0	717.931	8.282
2	80	36751.0	38440.0	459.388	-0.736
3	80	26590.5	38440.0	332.381	-5.167
4	80	23833.5	38440.0	297.919	-6.369
5	80	21916.0	38440.0	273.950	-7.205
6	80	24862.5	38440.0	310.781	-5.920

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
7	80	18818.5	38440.0	235.231	-8.555
8	80	34366.0	38440.0	429.575	-1.776
9	80	49565.0	38440.0	619.563	4.851
10	80	48028.0	38440.0	600.350	4.180
11	80	57245.0	38440.0	715.563	8.199
12	80	61869.5	38440.0	773.369	10.216

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
469.6276	11	<.0001*

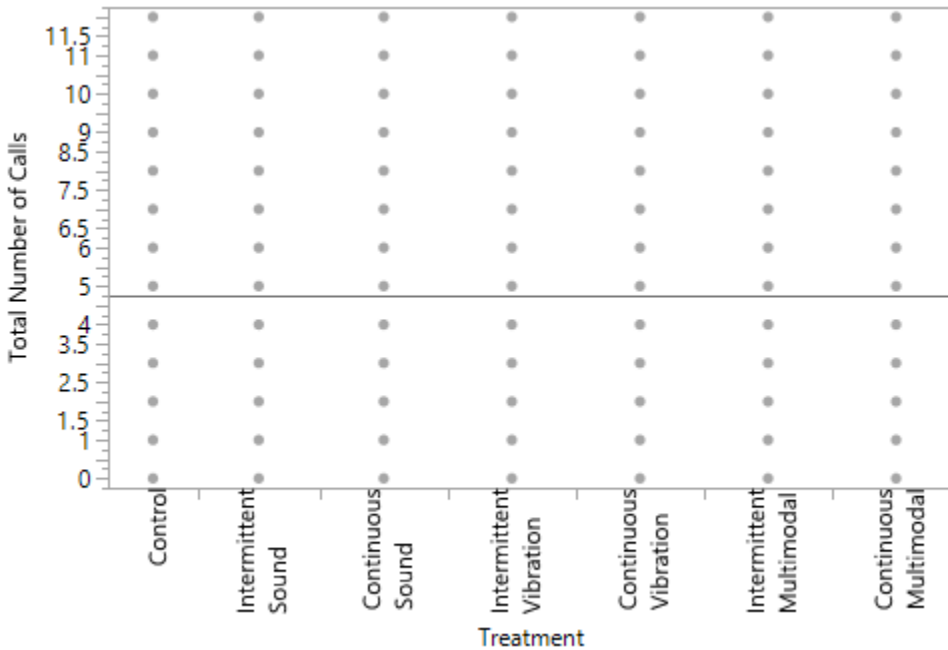
Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
12	7	538.125	42.34482	12.7082	<.0001*
12	5	499.406	42.34482	11.7938	<.0001*
11	7	480.319	42.34482	11.3430	<.0001*
12	4	475.438	42.34482	11.2278	<.0001*
12	6	462.575	42.34482	10.9240	<.0001*
11	5	441.600	42.34482	10.4287	<.0001*
12	3	440.975	42.34482	10.4139	<.0001*
11	4	417.631	42.34482	9.8626	<.0001*
11	6	404.769	42.34482	9.5589	<.0001*
9	7	384.319	42.34482	9.0759	<.0001*
11	3	383.169	42.34482	9.0488	<.0001*
10	7	365.106	42.34482	8.6222	<.0001*
9	5	345.600	42.34482	8.1616	<.0001*
12	8	343.781	42.34482	8.1186	<.0001*
10	5	326.388	42.34482	7.7079	<.0001*
9	4	321.631	42.34482	7.5955	<.0001*
12	2	313.969	42.34482	7.4146	<.0001*
9	6	308.769	42.34482	7.2918	<.0001*
10	4	302.419	42.34482	7.1418	<.0001*
10	6	289.556	42.34482	6.8381	<.0001*
9	3	287.169	42.34482	6.7817	<.0001*
11	8	285.975	42.34482	6.7535	<.0001*
10	3	267.956	42.34482	6.3280	<.0001*
11	2	256.163	42.34482	6.0494	<.0001*
8	7	194.331	42.34482	4.5893	0.0003*
9	8	189.975	42.34482	4.4864	0.0005*
12	10	173.006	42.34482	4.0857	0.0029*
10	8	170.763	42.34482	4.0327	0.0036*
9	2	160.163	42.34482	3.7823	0.0103*
8	5	155.613	42.34482	3.6749	0.0157*
12	9	153.794	42.34482	3.6319	0.0186*
10	2	140.950	42.34482	3.3286	0.0576
8	4	131.644	42.34482	3.1089	0.1240
8	6	118.781	42.34482	2.8051	0.3320
11	10	115.200	42.34482	2.7205	0.4302
8	3	97.181	42.34482	2.2950	1.0000
11	9	95.987	42.34482	2.2668	1.0000
12	11	57.794	42.34482	1.3648	1.0000

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
12	1	55.425	42.34482	1.3089	1.0000
6	5	36.819	42.34482	0.8695	1.0000
6	4	12.850	42.34482	0.3035	1.0000
11	1	-2.356	42.34482	-0.0556	1.0000
10	9	-19.200	42.34482	-0.4534	1.0000
6	3	-21.587	42.34482	-0.5098	1.0000
5	4	-23.956	42.34482	-0.5657	1.0000
8	2	-29.800	42.34482	-0.7037	1.0000
4	3	-34.450	42.34482	-0.8136	1.0000
7	5	-38.706	42.34482	-0.9141	1.0000
5	3	-58.419	42.34482	-1.3796	1.0000
7	4	-62.675	42.34482	-1.4801	1.0000
7	6	-75.537	42.34482	-1.7839	1.0000
7	3	-97.138	42.34482	-2.2940	1.0000
9	1	-98.356	42.34482	-2.3227	1.0000
10	1	-117.569	42.34482	-2.7765	0.3627
3	2	-126.994	42.34482	-2.9990	0.1787
6	2	-148.594	42.34482	-3.5091	0.0297*
4	2	-161.456	42.34482	-3.8129	0.0091*
5	2	-185.425	42.34482	-4.3789	0.0008*
7	2	-224.144	42.34482	-5.2933	<.0001*
2	1	-258.531	42.34482	-6.1054	<.0001*
8	1	-288.344	42.34482	-6.8094	<.0001*
3	1	-385.538	42.34482	-9.1047	<.0001*
6	1	-407.138	42.34482	-9.6148	<.0001*
4	1	-420.000	42.34482	-9.9186	<.0001*
5	1	-443.969	42.34482	-10.4846	<.0001*
7	1	-482.688	42.34482	-11.3990	<.0001*

Overall Comparisons

Oneway Analysis of Total Calls by Treatment



Wilcoxon/Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
Control	672	1572601	2146032	2340.18	-12.962
Intermittent Sound	913	3442848	2915666	3770.92	10.447
Continuous Sound	961	3147522	3068954	3275.26	1.524
Intermittent Vibration	960	3122790	3065760	3252.91	1.107
Continuous Vibration	960	2992552	3065760	3117.24	-1.421
Intermittent Multimodal	960	3614835	3065760	3765.45	10.657
Continuous Multimodal	960	2500544	3065760	2604.73	-10.970

Oneway Test ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
447.3423	6	<.0001*

Nonparametric Comparisons for All Pairs Using Dunn Method for Joint Rankings

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
Intermittent Sound	Control	1430.74	91.69531	15.6032	<.0001*
Intermittent Multimodal	Control	1425.27	90.73866	15.7074	<.0001*
Continuous Sound	Control	935.08	90.71922	10.3074	<.0001*
Intermittent Vibration	Control	912.73	90.73866	10.0588	<.0001*
Continuous Vibration	Control	777.06	90.73866	8.5637	<.0001*
Intermittent Multimodal	Continuous Vibration	648.21	82.34399	7.8720	<.0001*
Intermittent Multimodal	Intermittent Vibration	512.55	82.34399	6.2245	<.0001*
Intermittent Multimodal	Continuous Sound	490.20	82.32257	5.9546	<.0001*
Continuous Multimodal	Control	264.55	90.73866	2.9155	0.0746
Intermittent Multimodal	Intermittent Sound	-5.46	83.39700	-0.0655	1.0000
Intermittent Vibration	Continuous Sound	-22.35	82.32257	-0.2715	1.0000
Continuous Vibration	Intermittent Vibration	-135.66	82.34399	-1.6475	1.0000

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value
Continuous Vibration	Continuous Sound	-158.01	82.32257	-1.9195	1.0000
Continuous Sound	Intermittent Sound	-495.66	83.37584	-5.9449	<.0001*
Continuous Multimodal	Continuous Vibration	-512.51	82.34399	-6.2240	<.0001*
Intermittent Vibration	Intermittent Sound	-518.01	83.39700	-6.2114	<.0001*
Continuous Multimodal	Intermittent Vibration	-648.17	82.34399	-7.8715	<.0001*
Continuous Vibration	Intermittent Sound	-653.68	83.39700	-7.8381	<.0001*
Continuous Multimodal	Continuous Sound	-670.52	82.32257	-8.1451	<.0001*
Continuous Multimodal	Intermittent Multimodal	-1160.72	82.34399	-14.0960	<.0001*
Continuous Multimodal	Intermittent Sound	-1166.18	83.39700	-13.9835	<.0001*